SEED ECOLOGY IN MONTANE FORESTS ON O‘AHU: IMPLICATIONS FOR CONSERVATION

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF THE UNIVERSITY OF HAWAI‘I AT MĀNOA IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

IN

BOTANY
(ECOLOGY, EVOLUTION, AND CONSERVATION BIOLOGY)

AUGUST 2019

August 2019

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Keywords: Hawai‘i, restoration, seed dispersal, germination, invasive species, *Clidemia hirta, Rubus rosifolius, Alyxia stellata, Coprosma foliosa, Dianella sandwicensis, Leptecophylla tameiameiae*

Acknowledgments

Thank you to the Hawai‘i Vertebrates Introductions and Novel Ecosystems (VINE) Project, Hawai‘i Audubon Society, Ecology, Evolution, and Conservation Biology (EECB) Program, the Charles H. Lamoureux Fellowship in Plant Conservation, and the Dai Ho Chun Fellowship, for providing funding for my research. Thank you to the staff of the Department of Land of Natural Resources, Army Natural Resources Program, and Natural Area Reserve System, for providing access to field sites and logistical support, in particular Ryan Peralta, Marigold Zoll, and Kapua Kawelo. Thank you to the Mānoa Cliffs Restoration Project for allowing for access to the restoration site and sharing your constant enthusiasm for conservation.

Thank you to my committee for their generous feedback and support throughout this process: Don Drake, Kasey Barton, Cliff Morton, Marian Chau, and Amber Wright. Each member has helped improve my work as a scientist, and for that I am grateful. Special thanks to Don Drake, my committee chair, for always being available and willing to help and Amber Wright for serving as my University Representative and her additional support with statistical analyses.

Thank you to the Principal Investigators of the Hawai‘i VINE Project, Jeff Foster, Patrick Kelley, Corey Tarewater, and Jinelle Sperry, for their support and feedback. Thank you to Hawai‘i VINE Project Manager, Erika Dittmar, for support and logistical assistance. Thank you to Hawai‘i VINE graduate students and technicians for support and assistance in the lab and field: Arby Barone, Sam Case, Juliana Clark, Jason Gledistch, Jason DeLuca, Matt Jasper, Brandon Najarian, Dan Roche, Pia Ruisi-Besares, Patricia Sendao, Stephen Tyndel, Scott Van de Verg, Lindsey Wantanabe, and Becky Wilcox. A special thank you to Mio Shimada for her constant enthusiasm for sorting seeds under a dissecting scope. It has been a pleasure working with so many enthusiastic people and I look forward to future projects and collaborations.

Thank you to my friends for their never-ending love and support throughout this process. They've always been a light in dark times. Thank you to my family. To my parents, Dave and Karen, who have never lost faith in me and always been there – from my very first step to walking across the stage for my PhD. To my brother, Ryan, sister-in-law, Carrie, and niece, Paige, who have helped me balance focus with fun. To my sister, Kailey, whose sense of humor has always kept me smiling and is the definition of generous. Finally, to my partner, Jacob, who took a chance on my and moving to Hawai‘i and has never ceased to show me unconditional love. Thank you.

Abstract

Hawai‘i is renowned for its unique biota, and for the degree to which that biota is imperiled by extinction. Key threats to the native flora include alien herbivores, the loss of mutualists, and competition with alien species. Ecological restoration on the islands focuses on removing alien ungulates, reducing invasive alien plants, and increasing native diversity and recruitment. O‘ahu is the most populated island and has lost the highest proportion of forest cover compared to other main Hawaiian Islands. Forest communities are dominated by alien plants at lower elevations but retain increasing native diversity at higher elevations. All forest types have lost all native seed dispersers, which may significantly alter the recruitment of native species. Ongoing restoration efforts on O‘ahu, in combination with novel interactions between alien birds and both alien and native plants, provide a unique opportunity to investigate novel interactions and assess the effects of restoration efforts to reduce invasive alien plants and increase the recruitment of native plant species. I conducted three field studies on O‘ahu investigating various aspects of seed ecology.

In Chapter 2, I used seed rain traps and vegetation surveys, in three mixed and one native forest community, to investigate the distribution, reproduction, and dispersal of native and alien species adapted for bird dispersal. At all sites, alien seeds were more abundant in the seed rain and more frequently dispersed than native species, even where alien species made up <5% of the vegetation cover. Abundant alien species both in the vegetation and seed rain are among the most invasive alien species in the world. In Chapter 3, I measured and compared the seed rain and vegetation of native and alien bird-adapted species and the wind-dispersed native tree *Metrosideros polymorpha* in a three-year-old clear-cut surrounded by relatively intact forest to understand whether clear-cutting an invasive tree, *Psidium cattleyanum,* facilitates native plant regeneration. Two invasive alien understory species, *Clidemia hirta* and *Rubus rosifolius,* were

the most abundant species in the seed rain in both habitats and the most abundant vegetation in the clear-cut. Seeds of the dominant native tree, *Metrosideros polymorpha*, were dispersed into the clear-cut, but few seedlings occurred, possibly owing to microsite limitation. In Chapter 4, I investigated the effect of canopy cover on the germination and seedling survival of four common native plant species—*Alyxia stellata, Coprosma foliosa, Dianella sandwicensis,* and *Leptecophylla tameiameiae*—in a managed mesic forest. Germination of *A. stellata* and *C. foliosa* was positively correlated with canopy cover. Germination of *D. sandwicensis,* and *L. tameiameiae* was independent of canopy cover.

Invasive alien plants are regenerating more vigorously and more frequently dispersed than natives under current conditions. Two small-seeded alien species, *C. hirta* and *R. rosifolius,* are the most prolific invasive aliens in the seed rain and disperse into most forest microsites. Native recruitment is limited in all forest types and native species may benefit from human-mediated dispersal. Seed sowing in appropriate microsites is a potential method for increasing recruitment of common species.

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Chapter 1: Introduction

Island ecosystems are increasingly vulnerable to human disturbances, such as habitat loss and biological invasions (Sax & Gaines 2008; Kier et al. 2009). These disturbances have significantly increased extinction rates on islands and today many island ecosystems exist either as a mix of native and alien species or almost exclusively alien species (Meyer et al. 2015). Owing to a loss of key community members, many island ecosystems can no longer return to a historical state, but the novel assemblages of biota may sometimes continue to provide important ecosystem services (Rodriguez 2006; Hobbs et al. 2009; Mascaro et al. 2012). Understanding how these novel ecosystems function is critical for developing management priorities and strategies for these communities (Rodriguez 2006; Lindenmayer et al. 2008; Trueman et al. 2014).

A critical component of utilizing novel ecosystems is to identify species that provide and disrupt ecosystem services (Seastedt et al. 2008). Alien plant species can be major drivers of ecosystem degradation on islands, altering both ecosystem structure and function (Vitousek and Walker 1989; Asner and Vitousek 2005; Sax and Gaines 2008; Kueffer et al. 2010). Thus, removal of disruptive aliens can be critical for ecosystem structure and function; however, some aliens may functionally replace lost community members and increase ecosystem resilience (Ewel and Putz 2004; Seastedt et al. 2008; Cordell et al. 2016). In addition to removal of disruptive aliens, increasing native diversity and recruitment are critical components of ecological restoration on islands (Kueffer et al. 2010; Cordell et al. 2016).

Plant recruitment is ecologically complex, with many biotic and abiotic factors affecting seed dispersal, germination, and seedling establishment (*reviewed in* Beckman and Rogers 2013). Limitation may occur at one or more of these stages as a result of a variety of factors, such as loss of mutualists, competition, predation, or disturbance (Schupp et al. 2002; Aslan et al.

2013; Vargas and Stevenson 2013). Seed dispersal by animals is an important mutualism that promotes the recruitment of fleshy-fruited plant species (Traveset and Verdu 2002; Beckman and Rogers 2013). Dispersal mutualisms on islands are particularly vulnerable to disruptions because there are fewer mutualistic partners compared to continental ecosystems (Gonzalez-Castro et al. 2012). Many islands have been affected by the loss of dispersal mutualists, with potentially negative consequences for native plant populations (*e.g.,* Meehan et al. 2002; Chimera and Drake 2010; Wotton and Kelly 2011; Traveset et al. 2012; Culliney et al. 2015). Alien plants and animals can either facilitate the breakdown of mutualisms or functionally replace extinct mutualistic partners (*e.g.,* Mandon-Dalger et al. 2004; Gosper et al. 2005; Kawakami et al. 2009; McConkey et al. 2012; Traveset and Richardson 2014). Research on seed dispersal in heterogeneous landscapes at the community level would provide land managers with invaluable information regarding novel interactions and their effect on ecosystem structure and function (McConkey et al. 2012)

The Hawaiian Islands are renowned for both their incredible biodiversity and the impacts human settlement has had on their biota (Carlquist 1980; Mueller-Dombois & Fosberg 1998). Since human arrival, over 1,000 plant species have become naturalized (Wagner *et al.* 1999), with some species becoming invasive and causing community degradation (Daehler *et al.* 2004). Across the islands, efforts to conserve and restore native plants are ongoing (Friday et al. 2015), and it is estimated that federal, state, and private land management agencies spend approximately 75% of natural resource funding on the conservation and restoration of ecosystems to mitigate the damage caused by these invasive species (The Nature Conservancy 2003).

Primary restoration goals in Hawai‘i are to exclude alien ungulates, decrease the abundance of invasive alien plant species, and increase native plant diversity and recruitment

(*e.g.*, Cabin et al. 2000; Cabin et al. 2002a, 2002b; D'Antonio and Meyerson 2002; Cordell et al. 2008; Cordell et al. 2009; Ostertag et al. 2009). Natural recruitment is reported to be limited at either the seed or establishment stages in Hawai‘i and restoration areas often benefit from outplanting and seed additions (*e.g.*, Loh and Daehler 2008; Zimmerman et al. 2008; Brooks et al. 2009; Cordell et al. 2009; Ostertag et al. 2009; Inman-Narahari et al. 2013; Yelenik et al. 2016).

O‘ahu is the most populated Hawaiian island, and native forests no longer exist at low elevations; nevertheless, some forests still retain many native plants at higher elevations (including 65 species with fewer than 50 individuals left in the wild; Plant Extinction Prevention Program 2015). Most native flowering plant species in Hawaiian forests are fleshy-fruited and adapted for bird dispersal (Wagner et al. 1999; Sakai et al. 2002), but all native fruit-eating forest birds are extinct (Atkinson 1977), leaving only nonnative bird species (and possibly some nonnative mammals) to disperse seeds (Shiels & Drake 2011). Dispersal is a critical step for the recruitment of new individuals into plant populations; therefore, the current community of nonnative fruit-eating bird species may facilitate, or inhibit, the recruitment of native, fleshy-fruited plants (Foster & Robinson 2007; Chimera & Drake 2010). Research conducted to understand the roles of alien birds in the dispersal and recruitment of alien and native plants suggests that alien birds on O‘ahu eat primarily alien seeds; but little is known about the deposition of seeds they ingest (Garrison 2003; Vizentin-Burgoni et al. 2019). Ongoing restoration efforts on O‘ahu provide a unique opportunity to investigate novel interactions between alien birds and both alien and native plants, and assess the effects of restoration efforts to reduce invasive alien plants and increase the recruitment of native plant species.

In Chapter 2, I investigate the distribution, reproduction, and dispersal of alien and native plants, including wind-dispersed *Metrosideros polymorpha*, following the removal of a nearly

monospecific stand. Specifically, I ask: what fleshy-fruited species are most abundant in the vegetation? What is the annual fruit and seed production of fleshy-fruited species? What plant species are consumed and potentially dispersed by alien birds? How frequently do animals deposit seeds across landscapes? To answer these questions, I used seed traps and vegetation surveys to characterize the seed rain and vegetation in four mesic-wet forests on O‘ahu.

Chapter 3 is a case study investigating the dispersal and recruitment of native and alien plants following the clear-cut of invasive *Psidium cattleyanum*, including wind-dispersed *Metrosideros polymorpha*. *Metrosideros polymorpha* is the dominant early succession and mature forest tree in Hawai‘i (Mueller-Dombois and Fosberg 1998; Drake and Mueller-Dombois 1993). Thus *M. polymorpha* should be an important species regenerating in a clear-cut. In this chapter, I ask: are *M. polymorpha* and small-seeded, animal-dispersed seeds dispersing into the clear-cut? Does the seed rain of native and alien fleshy-fruited species differ between the clear-cut and the surrounding, relatively intact forest? If so, how? What species are regenerating in the clear-cut? I used seed rain traps and vegetation surveys in a relatively native mesic forest and clear-cut on O‘ahu to measure seed abundance and dispersal and plant cover.

In Chapter 4, I investigate the effect of canopy cover on the germination and seedling survival of four common fleshy-fruited species in a forest community undergoing restoration. Four under- to mid-story plant species (*Alyxia stellata, Coprosma foliosa, Dianella sandwicensis,* and *Leptecophylla tameiameiae*) were sown, and germination was monitored under different levels of canopy cover in a mesic forest.

With these combined studies, my dissertation broadly characterizes seed abundance and dispersal in novel forest communities on O‘ahu and investigates seed germination and the potential for seedling establishment in different microenvironments. Determining the abundances of seeds and how they disperse across the landscape provides a more comprehensive

understanding of the role of alien frugivores and the challenges involved in restoration efforts to facilitate native plant recruitment. Experimental germination and seedling survival under different levels of canopy cover can help predict suitable microhabitats for seed sowing. These data add to an extensive body of literature facilitating conservation and restoration efforts in Hawai‘i and can be used to help in adaptive management efforts across the islands.

Chapter 2: Alien songbirds facilitate species invasions in Hawaiian montane forests

Abstract

Species introductions and extinctions have altered islands worldwide. Loss of mutualistic partners and the formation of novel mutualisms between alien and native species may have drastic consequences, potentially facilitating invasions by alien species. The Hawaiian Islands have lost key seed dispersers, and native plants either partially or completely rely on alien dispersers; however, it is unclear to what extent alien birds facilitate or inhibit the regeneration of both alien and native plant species across the islands. We conducted vegetation surveys and used seed traps to compare the vegetation, seed production, and dispersal of all fleshy-fruited plant species in four forest communities on O‘ahu, where all native seed dispersers are extinct. All plant species dispersed were small-seeded (<10 mm), and most species produced multiple small seeds/fruit. At all sites, alien seeds were more abundant and frequently dispersed compared to native species, even where alien species made up <5% of the cover. Abundant alien species both in the vegetation and seed rain are among some of the most invasive alien species in the world. While alien birds are the only dispersers of small-seeded natives, they are predominantly vectors for invasive alien species. If novel ecosystems are utilized for conservation, creative methods will need to be developed to reduce the dispersal of invasive alien species.

Keywords: novel ecosystems, propagule pressure, seed dispersal, Hawai‘i

Introduction

Island communities are some of the most vulnerable to the introduction of alien species, with introductions contributing to the displacement and extinction of native species (Sax and Gaines 2008; Kueffer et al. 2010). As a result, many islands are now characterized by novel ecosystems that are either comprised of a mix of alien and native species or entirely of alien species (Sax and Gaines 2008; Meyer et al. 2015). Novel ecosystems are often unable to be returned to a historical state, owing to factors such as limited information about historical states, on-going human influence, or extinction of key community members; but, their unique assemblage of biota may continue to provide valuable ecosystem services, particularly on islands (Hobbs et al. 2009; Mascaro et al. 2012).

The extinction of community members means the loss of all ecological interactions associated with those species. All species are either directly or indirectly involved in one or more mutualistic partnership; thus one extinction can have cascading effects on the survival and reproduction of many organisms in a community (Bronstein et al. 2004). Theoretically, in novel ecosystems where species have gone extinct, surviving mutualistic partners will either share the same fate or form novel mutualisms with native or alien species that can take on the functional role of the extinct species (Aslan 2013). However, the loss of mutualistic partners often results in population declines (McConkey et al. 2012).

Seed dispersal by animals is an important mutualism which promotes the recruitment of fleshy-fruited plant species by dispersing them away from parent plants, potentially over long distances (Traveset and Verdu 2002; Beckman and Rogers 2013). Animal-mediated seed dispersal is particularly important in tropical systems where, animals are reported to disperse up to 90% of plant species (Farwig & Berens 2012, Jordano 2014). Seed dispersal mutualisms on islands are particularly vulnerable to disturbances and disruptions because they have fewer

interacting mutualistic species compared to continental mutualisms (Gonzalez-Castro et al. 2012). Many islands have been affected by the loss of dispersal mutualists, with potentially negative consequences for native plant populations (e.g., Meehan et al. 2002; Chimera and Drake 2010; Traveset et al. 2012; Culliney et al. 2012), and the addition of alien plants and animals can either facilitate the breakdown of mutualisms or functionally replace missing mutualistic partners (Gosper et al 2005; McConkey 2012; Traveset and Richardson 2014).

The Hawaiian Islands are an extreme example of an island system threatened by the introduction of alien species, because they are the most geographically isolated islands in the world, and are reported to have the highest number of introduced alien species of all Pacific islands (Mueller-Dombois & Fosberg 1998; Denslow et al. 2009). Since human arrival, over 1,000 plant species have become naturalized, including some of the most invasive species globally, roughly doubling the flora of Hawai‘i (Wagner et al.1999; Daehler and Carino 2000; Denslow et al. 2009). Few Hawaiian ecosystems, if any, have not been affected by the introduction of alien species which have contributed to the extirpation and/or extinction of many native species across the islands (Ziegler 2002).

Over half of the native flowering plant species in Hawaiian forests are fleshy-fruited and adapted for bird dispersal (Sakai et al. 2002; Price and Wagner 2004); thus, a loss of seed dispersers could inhibit their recruitment (Moran et al. 2009; Traveset et al. 2012). Research investigating the role of alien birds in Hawai‘i has demonstrated that alien birds incompletely compensate for lost native disperser services, but it is unclear to what extent alien birds facilitate or inhibit the recruitment of native and alien fleshy-fruited plants (Foster & Robinson 2007; Chimera & Drake 2010; Shiels & Drake 2011; Pejchar 2015, Kaushik et al. 2018). Loss of dispersal mutualists in Hawaiian forests may contribute to recruitment limitation and failure (Inman-Narahari 2011).

O‘ahu is arguably the most disturbed main Hawaiian Island, and represents an extreme within the archipelago when it comes to human population, introduced species, and novel ecosystems. Native-dominated forests no longer exist at low elevations; nevertheless, forests still retain many native plants at higher elevations. All native, frugivorous forest birds are extinct on O‘ahu (Atkinson 1977), leaving only alien bird species (and possibly some alien mammals) to disperse seeds (Shiels & Drake 2011). Research conducted on O‘ahu to understand the roles of alien birds in the dispersal and recruitment of alien and native plants suggests that alien seeds are the main dietary item of alien birds; but little is known about the deposition of seeds on the landscape post-ingestion (Garrison 2003; Vizentin-Burgoni et al. 2019).

We worked in four forest communities to investigate the distribution, reproduction, and dispersal of native and alien fleshy-fruited (bird-adapted) species on O‘ahu. One forest community was considered “native” because fleshy-fruited alien species made up less than five percent of the plant cover. Three forests were “mixed” because alien fleshy-fruited plants comprised greater than 50% of the plant cover. Specifically, we asked in mixed and native forest communities: what fleshy-fruited species are most abundant in the vegetation? What is the annual fruit and seed production of fleshy-fruited species? What plant species are being consumed and potentially dispersed by alien birds? How uniformly bird-dispersed seed distributed across landscapes? We used a combination of vegetation surveys and seed traps to investigate the cover, fruit and seed abundance, and potential seed dispersal of alien and native species. We predicted that alien seeds would be more uniformly dispersed across the landscape than native seeds because of high fruit abundance and accessibility across the landscape. We also predicted that alien birds would incompletely replace historic frugivores and disperse only small seeded (<10 mm) species, because of their smaller gape size compared to historic native fruit-eating birds (Culliney et al. 2012).

Methods

Study Sites

We surveyed vegetation and quantified seed rain and dispersal in one native and three mixed montane forest communities on O‘ahu, Hawai‘i (Table 1). Owing to differences in topography, elevation, rainfall, and history, vegetation varied among sites. Pahole (PAH) and Kahanahāiki (KAH) are mesic forests, Tantalus (TAN) is a wet forest, and Mount Ka‘ala (MTK) is a very wet, stunted forest with a canopy mostly < 4 m in height (DLNR 1981; Mueller-Dombois & Fosberg 1998). All sites had wind-dispersed *Metrosideros polymorpha* as an abundant native species in the canopy (absolute cover: TAN: 5.4 %, PAH: 18.3%, KAH: 27.8 %, and MTK: 23.8%; *unpublished data*). Mixed sites also had native *Acacia koa* in the canopy (TAN: 4.2%, PAH: 0.2%, KAH: 9.3%; *unpublished data*) and various alien canopy species, including fleshy-fruited *Psidium cattleyanum, Schinus terebinthifolius, Cinnamomum burmannii,* and *Bischofia javanica.* All sites had a midstory with common fleshy-fruited native species, such as *Alyxia stellata, Kadua affinis, Psydrax odorata,* and *Psychotria mariniana*. All sites are actively managed to varying degrees: TAN by grass-roots volunteers and the Department of Land and Natural Resources (DLNR), KAH by O‘ahu Army Natural Resources Program (OANRP), and MTK and PAH by DLNR and OANRP.

Vegetation Sampling

Point intercept transects were used to determine percent cover of plant species at each site (Mueller-Dombois and Ellenberg 1974). Transect layout and area sampled were constrained by topography and thus varied by site (Table 3). At PAH, transects were laid out in a stratified-random pattern perpendicular to a main trail throughout the site. AT KAH, transects were oriented parallel to small management trails in a grid pattern. At TAN, four parallel transects traversed the site. At MTK, transects were along a central boardwalk and management trails.

Every meter, cover was measured along a vertical line in three separate strata: understory (0-2 m), midstory (>2-4 m), and canopy (>4 m). Our vertical line at 0-4 m and > 2-4 m was measured using a 1.3-cm-diameter pole. Measurements >4 m were taken with a moosehorn densitometer. Within a stratum, species were counted only once per point, even if multiple individuals were intercepted.

Seed Diversity, Abundance, and Dispersal

One hundred and eight to 150 seed traps were used to capture seed rain at each site. Traps were spaced 5-10 m apart, along the vegetation transects (Table 3). Traps were constructed from plastic 24.5-cm-diameter pots covered with poultry wire with 2.5 cm hexagonal openings to limit animal access to fruits and seeds within the traps (Drake 1998). Samples were collected approximately every four to eight weeks from September 2015-October 2016, then dried and identified to genus and species under a dissecting microscope. Annual seed rain includes seeds within whole or partial fruits, and seeds outside of fruits. For whole fruits with multiple seeds, seed abundance was estimated using either a mean number of seeds/fruit based on field collections or data provided by Wagner et al. (1999) (Appendix 1). To estimate how seeds are possibly dispersed at each site, all fleshy-fruited seeds within a sample were categorized as "animal-handled" or "not animal-handled". Seeds were classified as animal-handled if they were either in animal feces or were not found within a fruit and there were no whole or partial fruits present in same trap sample. This is a conservative measure of animal-handling because seeds not found within a fruit but in a sample with whole or partial fruits were categorized as not animal-handled.

Results

Vegetation

MTK had the highest ratio of native: alien fleshy-fruited species (17:1) and TAN had the lowest (1:2.4; Table 3). At MTK, the only alien species (*Rubus argutus*) recorded comprised 1.5% of the understory and < 1.5% of the mid-story (Table 2). The natives with the greatest cover at MTK were *Broussaisia arguta*, *Dianella sandwicensis*, and *Leptecophylla tameiameiae* (Table 2). Alien species were more abundant than native species across all strata of mixed sites, except the herbaceous layer at KAH (Figure 1). At PAH and KAH, *Clidemia hirta*, *Psidium cattleyanum*, and *Schinus terebinthifolius* were the most abundant aliens, and *Alyxia stellata*, *Coprosma foliosa*, *Kadua affinis*, and *Psydrax odorata* were the most abundant natives (Table 2). At TAN, *Hedychium* sp., *Coffea arabica*, and *Cinnamomum burmannii* were the most abundant alien species and *Pipturus albidus*, *Psychotria marinana*, *Antidesma platyphyllum* and *Touchardia latifolia* were the most abundant natives (Table 2).

Total Seed Rain

Seed traps captured 1,614,081 total seeds (273,181 loose seeds + 8,370 whole fruits), representing 18 native species, 21 alien species, and three unidentified morphotypes. MTK had the highest ratio of native: alien species richness (2.3:1) and TAN had the lowest (1:2.4; Table 3). At all sites, there were more alien than native seeds that expected based on the proportion of species cover in the vegetation (Figure 2). Alien seeds were three times more abundant than natives at MTK and approximately 40, 1000, and 6000, times more abundant than natives at TAN, KAH, and PAH, respectively (Figure 2). Alien seeds were more abundant than native seeds during two months of the year at MTK and more abundant in all months at PAH, KAH, and TAN (Appendix 2). All alien species recorded in the vegetation were also captured by traps and *Clidemia hirta*, *Rubus rosifolius*, and *Psidium cattleyanum* were the most abundant aliens

captured at each site (Table 2). In contrast, many native species recorded in the vegetation were not captured. At MTK, Species present with >1.5% absolute cover but not found in the seed rain included: *Coprosma ochracea, Ilex anomala,* and *Smilax melastomifolia* (Table 2). At TAN, PAH, and KAH, many species that made up >1.5% of the vegetation were not captured by traps including *Coprosma foliosa, Diospyros* spp., and *Psydrax odorata* (Table 2).

Animal-handled Seed Rain

Animal-handled seeds in the traps represent seeds potentially dispersed by alien vertebrates. Fourteen alien species and twelve native species were animal-handled across sites. MTK had the highest native:alien ratio of species (2.3:1) and TAN had the lowest (1:2.2; Table 3). Animal-handled alien seed were captured in 100% of traps at TAN, PAH, and KAH and in 48% of traps at MTK (Figure 3). Animal-handled native seeds were captured by less than 45% of traps at all sites (Figure 3). Only three animal-handled native species occurred in >10% of traps at all sites: native *Brousassia arguta* (MTK: 28%) and *Vaccinium calycinum* (MTK: 14%) and *Pipturus albidus* (TAN: 31.5%). Two animal-handled alien species, *Clidemia hirta* and *Rubus rosifolius,* occurred in >80% of traps at TAN, PAH, and KAH. At MTK, animal-handled *Clidemia hirta* seeds were captured in >40% of traps.

At TAN, PAH, and KAH all traps captured at least one animal-handled alien species, with most traps capturing 2-4 species (Figure 4). At MTK, < 30% of traps captured one or more animal-handled native species (Figure 4). At MTK almost 50% of traps captured at least one alien species handled by animals (Figure 4). At PAH and KAH > 90% of traps did not capture an animal-handled native species; however, 42% of traps captured 1-2 animal-handled native species (Figure 4).

For all alien species, at least some (and sometimes most) seeds had been animal-handled. At MTK, approximately 80% of *Rubus argutus,* the only alien species in the vegetation, were

animal-handled (Table 3). At TAN, PAH, and KAH, greater than 60% of all *Rubus rosifolius* seeds were animal-handled (Table 3). Other alien species for which greater than 50% of seeds had been animal-handled at one or more sites included *Psidium guajava, Passiflora suberosa, Hedychium gardnerianum,* and *Schinus terebinthifolius* (Table 3). Additionally, traps captured animal-handled species not recorded during vegetation surveys at a given site: *Clidemia hirta* and *Rubus rosifolius* at MTK and *Trema orientalis* at TAN (Table 3).

All native species captured by traps at MTK were animal-handled, and *Broussaisia arguta, Dianella sandwicensis,*and *Pipturus albidus,* had 45% or greater of their seeds categorized as being animal-handled (Table 3). At TAN, PAH, and KAH not all native species in traps were animal-handled. *Alyxia stellata,* a common large-seeded species in the vegetation and seed rain, was not animal-handled (Table 3). Conversely, native species that accounted for >1% of total native seed rain with >50% of seeds categorized as animal-handled included *Antidesma platyphyllum, Clermontia kakeana, Cyanea angustifolia,* and *Pipturus albidus* (Table 3).

All animal-handled species are small-seeded (<9 mm diameter) and most also produce many seeds/fruit. Six of seven alien species and six of eight native species with >50% animal-handled seeds at one or more sites produce fruits with multiple seeds (Table 3; Appendix 1). Across sites, the smallest animal-handled alien seed was *Clidemia hirta* (0.5 mm) and the largest was *Psidium cattleyanum* (5.1 mm). The smallest native animal-handled seeds were *Cyanea angustifolia* and *Cyrtandra cordifolia* (0.5 mm), and the largest was *Antidesma platyphyllum* (8.9 mm).

Discussion

Across all forest types on O‘ahu, a higher number of alien seeds than native seeds were handled by animals, and they were captured in a higher proportion of traps. Since animal-handled seeds could potentially result in a dispersal event, alien plants are likely being dispersed

to more microsites, and in higher quantities, compared to native plants across the island. At MTK native species were more abundant in the vegetation, but animal-handled alien seeds were still more abundant and dispersed into more traps than natives. Alien species most frequently found in the vegetation, seed rain, and potentially dispersed by alien birds represent some of the world's most invasive species (*e.g. Clidemia hirta, Psidium cattleyanum, Schinus terebinthifolius*) (Daehler et al. 2004; Lowe et al. 2000). *Clidemia hirta* and *Rubus rosifolius* were two small-seeded (<10 mm) invasive alien species found in 69-100% of all traps at TAN, PAH, and KAH after being handled by animals.

Native species were dispersed less frequently compared to aliens, but those species that were dispersed often had a high proportion of their seeds dispersed. In contrast, many native species were not captured by seed traps, despite some being relatively common in the vegetation. Species found in the vegetation without being captured in the seed rain included *Coprosma foliosa, Diospyros sandwicensis,* and *Psydrax odorata. Coprosma foliosa* is a small-seeded dioecious species that I would have expected to potentially be dispersed by alien birds (Wagner et al 1999). Seeds of *Psydrax odorata* are commonly attacked by the moth larvae, *Orneodes objurgatella*, and seed viability lower than 10% has been reported (Criley 1998). *Diospyros sandwicensis* is a large-seeded species well-known to be depredated by invasive rats in Hawai‘i (Shiels and Drake 2011).

Potential factors influencing dispersal by alien birds

Resource abundance and phenology can be important predictors for bird diet, particularly in generalist species (e.g., Rey 1995, Gleditsch and Carlo 2010). Resource availability can affect species interactions in space and time, thus affecting seed dispersal in space and time (Gleditsch et al. 2017). Alien frugivores on O‘ahu are considered to be generalists with little known about how species abundances affect their diet (Vizentin-Bugoni et al. 2019). Across sites, alien seeds

are more abundant than native seeds on the landscape, and a high number of animal-handled alien seeds in the seed rain may be the result of a high abundance of reproductive plants in the vegetation, high fruit abundance, and/or a high number of seeds/fruit. Native seed abundance was much lower at all sites, ranging from 10s-100s of seeds per m2. Although native seeds were not as abundant on the landscape, species that did have high proportions of their annual seed rain dispersed were some of the most abundant in the vegetation at their respective sites.

Additionally, fruit and seed traits are also considered important for predicting dispersal and recruitment patterns in ecosystems and may be increasingly important for assessing novel interactions (Westoby et al. 1996; Fricke et al. 2019; Vizentin-Bugoni 2019). Birds cannot ingest, and subsequently disperse, seeds larger than the size of their gape (Wheelwright 1985); thus, we expected that alien songbirds on O‘ahu would not be able to disperse seeds over 10 mm because of their gape size. Alien birds would also be able to disperse only a subset of the native flora because of their smaller gape size compared to historic birds (Culliney et al. 2012; Wu et al. 2014; Walther & Hume 2016). I found that all native and alien species categorized as animal-handled were small-seeded (<10 mm). Furthermore, both native and alien species that produced numerous small seeds per fruit had a higher percentage of their seeds categorized as animal-handled, suggesting that many seeds/fruit may be an important trait for predicting dispersal patterns by alien birds in Hawaiian forests.

Resource abundance and fruit and seed functional traits are not mutually exclusive and both may affect the proportion of seeds dispersed by alien birds. Species that produce larger fruit crops of small-sized seeds have a greater probability of being removed by birds at higher rates and deposited into more seed traps than? (Howe and Estabrook 1977; Izhaki 2002).

Alien birds as dispersers of native seeds

Animal-handled native seeds were less abundant compared to alien seeds and were in fewer traps at all sites. That small-seeded native species dispersed into low frequencies of traps suggests that bird-dispersed native species are more clustered on the landscape (Rose et al. 2017). Birds did not disperse large-seeded species and since current alien dispersers are likely not capable of dispersing larger-seeded native species, it is likely that large-seeded natives are dispersal limited and seeds primarily fall below the parent plant.

Lack of dispersal could have several negative consequences for native plant species. Seeds that occur at higher densities under parent trees may be subjected to higher levels of depredation than? (*e.g.*, Wenny 2000; Moles and Drake 1999). Chimera and Drake (2011) found that Hawaiian native species that did not disperse away from parent plants on Maui were more likely to be depredated than dispersed seeds, potentially contributing to recruitment failure. Additionally, seedlings that occur at high densities below parent plants are likely to experience higher rates of mortality because of density-dependent seedling depredation, competition, or greater exposure to pathogens from the parent plant (e.g., Augspurger 1984; Hansen et al. 2008; Wotton and Kelly 2011). Additionally, alien birds may be depositing seeds in either favorable or poor microsites, particularly in mixed forests where alien species in the vegetation likely create unfavorable microsites; thus, research investigating deposition environments of native seeds is increasingly important (McConkey et al. 2012; Yelenik 2016).

Alien birds facilitating invasive plants in Hawai‘i

Most research in Hawaiian forests investigating seed dispersal by alien birds has found similar, albeit less dramatic, trends of alien birds contributing to the spread of invasive alien plants. Most notably, studies on Hawai‘i Island and Kaua‘i found that sites with one native and multiple alien bird dispersers had fewer alien and more native species dispersed into traps compared to similar sites without a native disperser (Pejchar 2015; Kaushik et al. 2018). On

Maui, where native dispersers are also extinct, Chimera and Drake (2009) found that alien birds dispersed predominantly alien seeds in dry forest, likely facilitating the spread of invasive species. However, Foster and Robinson (2007) investigated seed dispersal in a mixed and native forest community patch on Maui and found alien birds dispersed more native seeds than alien seeds and potentially were an important disperser for native species into degraded habitats. Our research supports that alien birds are potentially important dispersers of small-seeded native plants, but they are predominant dispersers of invasive alien seeds in these sites.

Invasive alien seeds arrived into a majority of traps because of animal-handling suggesting that propagule pressure is likely an important component of invasion success in O‘ahu forests, specifically for *Clidemia hirta* and *Rubus rosifolius* (Lockwood et al. 2005; Simberloff 2009). In particular, the higher frequency of alien than native seeds dispersed into MTK from outside the site demonstrates that alien birds are responsible for continually introducing invasive seeds into forests where these species are otherwise rare. The high frequency of dispersed invasive alien seeds suggests that these plants are either abundant across the landscape or repeatedly visited outside MTK and brought into the site by birds (Rose et al. 2017). Since alien birds have been found to interact predominantly with alien species on O‘ahu (Vizentin-Bugoni 2019), and we found seeds dispersed into a high percentage of traps at MTK, it is possible that alien birds may be seeking out abundant alien plant species.

Conclusion

Given the variability in the composition of these novel ecosystems through space and time and a limited understanding of existing and/or lost mutualisms, further research is required to understand novel ecosystems and manage them for conservation (Lindenmayer et al. 2008; Trueman et al. 2014). Our findings suggest that land managers and conservation practitioners in Hawai‘i should be mindful of alien birds as potential dispersers of both native and alien seeds.

Alien birds are the sole dispersers of small-seeded native species and perhaps increasing the abundance of small-seeded native species on the landscape could increase their dispersal by alien birds and subsequent regeneration (Yelenik 2016). However, creative solutions to remove reproductive invasive alien species will be needed to reduce the overall impact of their seed production in novel ecosystems. Managers should continue to invest in invasive species removal even if alien species are rare or have seemingly been removed from the forest vegetation because alien birds disperse invasive alien seeds into native environments.

Tables

Table 1.1 The classification, location, elevation, and mean annual rainfall of the four sampled forest sites. Rainfall from Giambelluca *et al*. (2013).

Site	Forest Type	Mountain Range	Latitude	Longitude	Elevation (m)	Rainfall (mm)
Tantalus (TAN)	Mixed	Koʻolau	21°20'18.19"N	157°48'39.29"W	549	3421
Pahole (PAH)	Mixed	Waiʻanae	21°32'11.30"N	158°10'47.64"W	594	1533
Kahanahāiki (KAH)	Mixed	Waiʻanae	21°32'12.55"N	158°11'35.40"W	667	1345
Mount Kaʻala (MTK)	Native	Waiʻanae	21°30'24.58"N	158° 8'41.17"W	1206	1953

Table 1.2 The percent cover, total annual seed rain, and animal-handled seed rain of species that made up > 1.5% of cover or > 1% of the total alien or native seed rain at one or more sites. The absolute percent cover for each species corresponds to the stratum in which it had its greatest percent cover (Appendix 1). Annual seed rain is the total number of seeds captured per m^2 and includes seeds found in whole or partial fruit, or outside fruit (including animal-handled seeds). Animal-handled seeds are seeds that occurred in fecal material or occurred outside fruit in a sample containing no whole or partial fruits.

	% Cover				Total Annual Seed Rain				Animal-handled Seeds				% Animal-handled			
Species	**TAN**	**PAH**	**KAH**	**MTK**	**TAN**	**PAH**	**KAH**	**MTK**	**TAN**	**PAH**	**KAH**	**MTK**	**TAN**	**PAH**	**KAH**	**M**
Alien																
Bischofia javanica	6.2	0.0	0.0	0.0	350.2	0.0	0.0	0.0	8.7	0.0	0.0	0.0	2.5	--	--	
Cestrum nocturnum	5.1	0.0	0.0	0.0	2.7	0.0	0.0	0.0	0.4	0.0	0.0	0.0	16.7	--	--	
Cinnamomum burmannii	27.6	0.0	0.0	0.0	119.6	0.0	0.0	0.0	41.2	0.0	0.0	0.0	33.1	--	--	
Clidemia hirta	6.7	14.2	21.1	0.0	3,951	190,000	26,751	713.3	963.1	4,799	5,208	79.0	28.0	2.4	19.5	1
Coffea arabica	7.2	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	--	--	
Ficus microcarpa	3.5	0.0	0.0	0.0	7,430	0.0	0.0	0.0	281.2	0.0	0.0	0.0	3.8	--	--	
Hedychium spp	15.7	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.7	0.0	0.0	0.0	83.4	--	--	
Passiflora suberosa	0.0	0.1	1.8	0.0	0.0	1.6	3.3	0.0	0.0	1.6	2.3	0.0	--	100.0	68.8	
Psidium cattleyanum	0.3	27.5	12.1	0.0	17.2	1,985	810.0	2.2	12.7	142.9	22.9	0.0	73.9	7.2	2.7	(
Psidium guajava	0.3	4.0	0.0	0.0	227.0	140.9	0.4	0.0	227.0		0.4	0.0	100.0	12.0	100.0	
Rubus argutus	0.0	0.0	0.0	1.5	0.0	0.0	0.0	1.3	0.0	0.0	0.0	2.8	--	--	--	7
Rubus rosifolius	3.5	2.4	0.8	0.0	82.2	949.8	1,331	2.1	82.2	778.1	824.6	2.1	100.0	81.9	61.9	1(
Schinus terebinthifolius	0.0	36.6	8.5	0.0	0.3	1,546	103.2	0.0	0.0	57.0	5.5	0.0	0.0	68.0	5.1	
Trema orientalis	0.0	0.0	0.0	0.0	3.3	0.0	0.0	0.0	3.3	0.0	0.0	0.0	100.0	--	--	
Alien Total	--	--	--	--	12,186	194,622	29,000	718.9	1,620	5,778	6,064	83.9	13.3	0.3	20.9	1
Native																
Alyxia stellata	0.0	13.2	30.9	0.0	0.0	1.5	6.1	0.1	0.0	0.0	0.0	0.0	--	0.0	0.0	

Antidesma platyphyllum	0.8	0.2	0.0	0.0	6.6	0.0	0.0	0.0	6.6	0.0	0.0	0.0	100.0	--	--	
Broussaisia arguta	0.0	0.0	0.0	11.7	0.0	0.0	0.0	68.2	0.0	0.0	0.0	37.3	--	--	--	4
Cheirodendron platyphyllum	0.0	0.0	0.0	3.3	0.0	0.0	0.0	2.2	0.0	0.0	0.0	0.1	--	--	--	6
Clermontia kakeana	0.3	0.0	0.0	0.0	5.2	0.0	0.0	0.0	5.2	0.0	0.0	0.0	100.0	--	--	
Coprosma foliosa	0.0	2.4	10.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	--	0.0	0.0	
Coprosma ochracea	0.0	0.0	0.0	1.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	--	--	--	0
Cyanea angustifolia	0.0	0.0	0.0	0.0	115.9	0.0	0.0	0.0	75.9	0.0	0.0	0.0	65.5	--	--	
Dianella sandwicensis	0.0	0.0	0.0	20.3	0.0	0.0	0.0	8.1	0.0	0.0	0.0	5.0	--	--	--	6
Diospyros hillebrandii	0.0	2.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	--	0.0	--	
Diospyros sandwicensis	0.0	0.5	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	--	--	0.0	
Ilex anomala	0.0	0.1	0.0	5.2	0.0	0.1	0.0	0.0	1.6	0.0	0.0	0.0	52.3	0.0	--	0
Kadua affinis	0.0	1.3	3.1	0.0	0.0	4.4	17.0	1.6	0.0	0.0	1.0	0.1	--	0.0	6.4	9
Leptecophylla tameiameiae	0.0	0.0	0.0	18.8	0.0	0.4	0	69.4	0.0	0.3	0.0	0.3	--	66.7	--	0
Pipturus albidius	2.2	0.5	0.0	0.0	115.2	27.0	0.0	0.3	97.7	0.7	0.0	0.3	84.9	2.7	--	10
Psychotria mariniana	1.2	2.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.0	0.0	100.0	--	
Psydrax odorata	0.0	0.2	3.9	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	--	0.0	0.0	
Smilax melastomifolia	0.0	0.0	0.0	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	--	--	--	0
Touchardia latifolia	1.0	0.0	0.0	0.0	37.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	--	--	
Vaccinium calycinum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.2	0.0	0.0	0.0	15.3	--	--	--	1
Wikstroemia oahuensis	0.0	0.2	1.5	0.0	0.0	0.0	6.6	0.0	0.0	0.0	0.0	0.0	--	0.0	0.0	
Native Total	--	--	--	--	280.2	33.5	30.3	250.1	187	1.1	1	58.4	66.7	3.3	3.3	2
Alien + Native Total	--	--	--	--	12466.2	1904657.2	29030.4	969.0	1807.5	5779.7	6065.1	142.3	14.5	0.3	20.99	1

Table 1.3 The sampling effort and resulting native and alien species richness for fleshy-fruited species in the vegetation and seed rain at each site. Annual seed rain is the total number of seeds captured per m^2 and includes seeds found in whole or partial fruit, or outside fruit (including animal-handled seeds). Animal-handled seeds are seeds that occurred in fecal material or occurred outside fruit in a sample containing no whole or partial fruits. Total points are the number of sampling points taken at each site using point-intercept methods. Trap number is the number of seed traps at each site.

	Vegetation			***Annual Seed Rain***				
					Total Seed Rain		***Animal-Handled Seed Rain***	
Site	**Total Points**	**Native Richness**	**Alien Richness**	**Trap Number**	**Native Richness**	**Alien Richness**	**Native Richness**	**Alien Richness**
TAN	585	8	19	146	7	13	6	13
PAH	1265	31	10	150	10	7	5	7
KAH	460	13	5	108	6	6	2	6
MTK	600	17	1	150	9	4	7	3

Figures

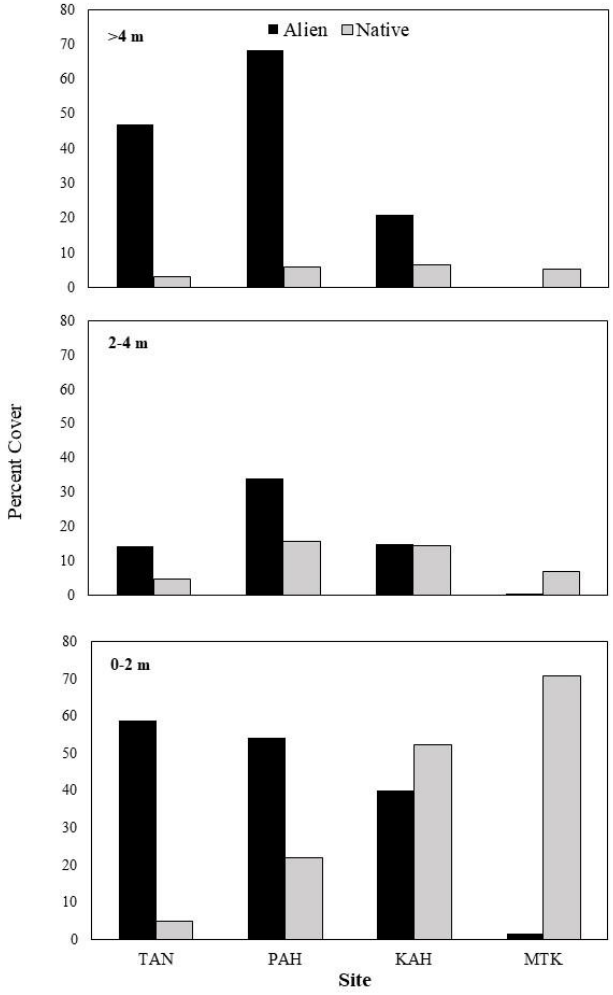


Figure 1.1 Percent cover of alien and native fleshy-fruited species in the vegetation in the understory (0-2 m), midstory (2-4 m), and canopy (>4 m) at each site. TAN, PAH, KAH are mixed communities (vegetation has >50% alien species cover) and MTK is a native forest community (<5% alien species cover). All mixed communities are mesic to wet montane forest communities and MTK is a wet montane stunted forest with few trees reaching the canopy (>4 m) strata.

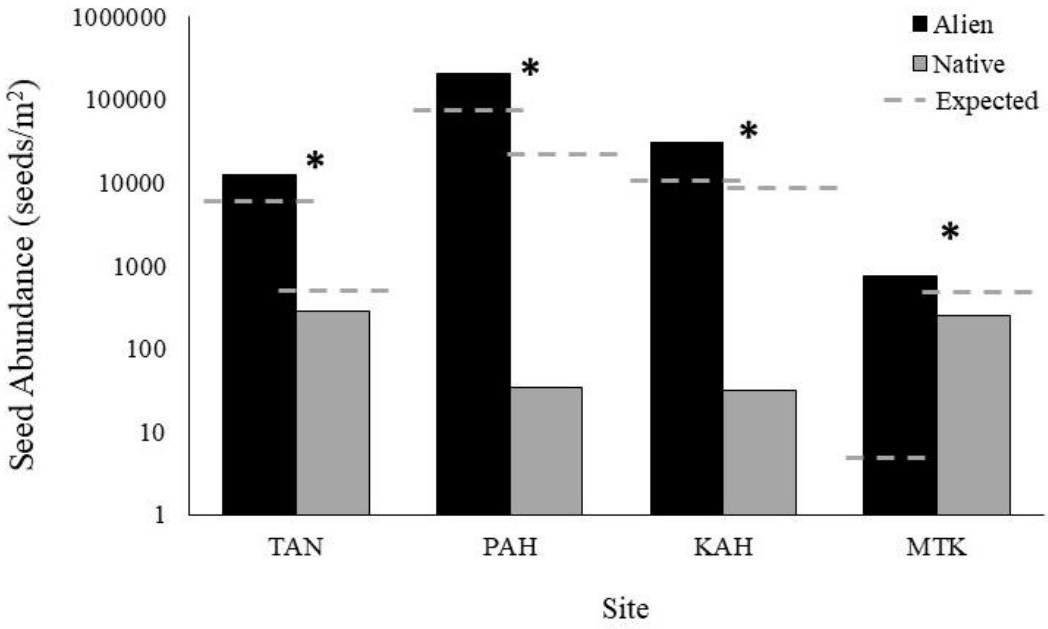


Figure 1.2 The annual seed rain of fleshy-fruited alien and native species compared to the vegetation at each site. Annual seed rain is the total number of seeds captured per m^2 and includes seeds found in whole or partial fruit, or outside fruit (including animal-handled seeds) and is presented on a logarithmic scale to compare native (100s of seeds) and alien seeds (1000s of seeds). The dashes line represents the expected annual seed rain of fleshy-fruited species if seed production was proportional the cover of alien and native species in the vegetation. TAN: χ^2: 832.8, $p < 0.001$; PAH: χ^2: 54817, $p < 0.001$, KAH: χ^2:27773, $p < 0.001$; MTK: χ^2:25727, $p < 0.01$.

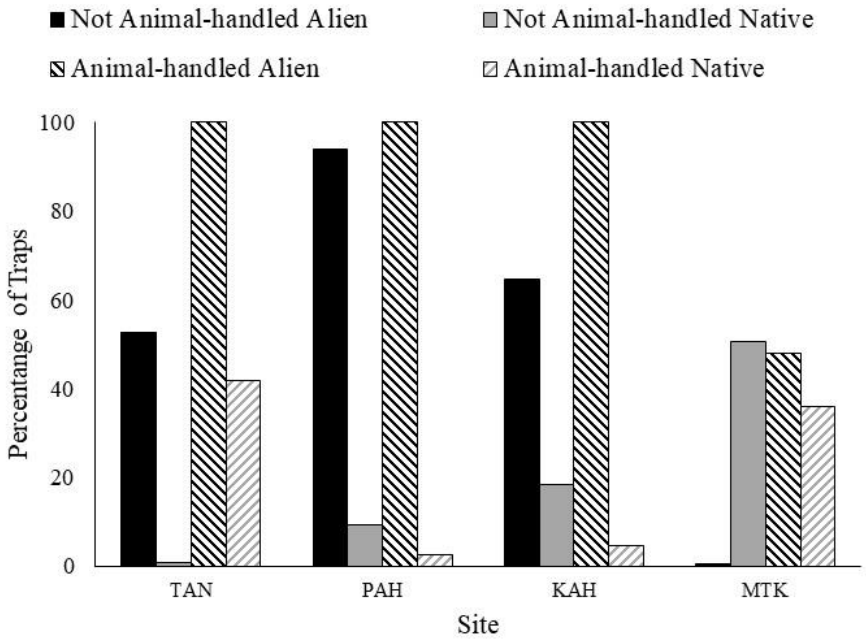


Figure 1.3 The percent of seed traps in which alien and native seeds were captured. TAN, PAH, and KAH are sites with mixed sites with > 50% alien cover and MTK is a native site with <5% alien cover. TAN had 146 traps, PAH had 150 traps, KAH had 108 traps, and MTK had 150 traps.

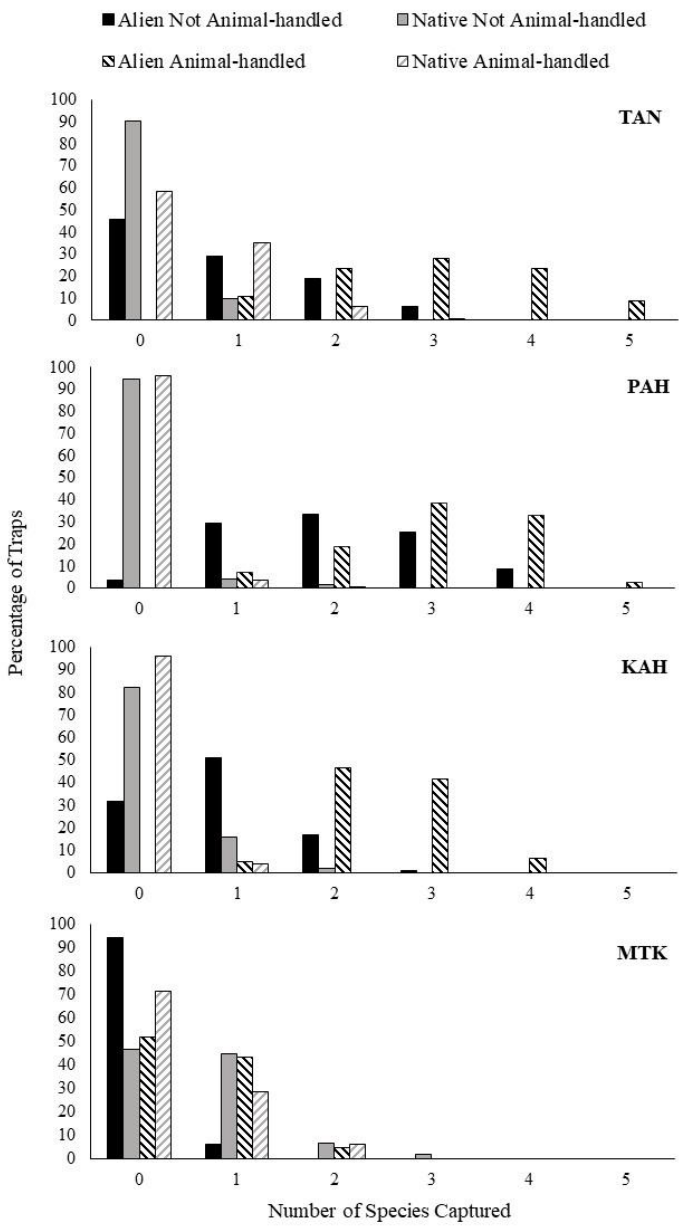


Figure 1.4 The frequency distribution of number of species captured per seed trap by site. TAN, PAH, and KAH are sites with mixed sites with > 50% alien cover and MTK is a native site with <5% alien cover. TAN had 146 traps, PAH had 150 traps, KAH had 108 traps, and MTK had 150 traps. Appendix 3 lists the most frequently captured animal-handled species.

Chapter 3: Clear-cut of invasive *Psidium cattleyanum* facilitates understory alien species on O‘ahu, Hawai‘i

Abstract

Invasive tree species can create dense monocultures that alter ecosystem structure and function. Removing such forest stands and restoring native vegetation is time intensive and expensive. Clear-cutting invasive trees is one method for potentially promoting native plant regeneration. To understand whether clear-cutting a stand of the invasive tree *Psidium cattleyanum* facilitates native plant regeneration in Hawai‘i, I measured and compared the seed rain and vegetation of native and alien fleshy-fruited species and the wind-dispersed native tree *Metrosideros polymorpha* in a three-year-old clear-cut surrounded by relatively intact forest. Two invasive alien understory species, *Clidemia hirta* and *Rubus rosifolius,* were the most abundant species in the seed rain in both habitats and the most abundant vegetation in the clear-clear cut. Excluding *C. hirta* and *R. rosifolius,* a greater proportion of fleshy-fruited native and alien species were dispersed by birds in the clear-cut compared to the forest, but seeds of alien species were more abundant than those of natives. Seeds of the dominant native tree, *Metrosideros polymorpha,* were dispersed into the clear-cut, but few seedlings occurred, probably owing to microsite limitation. Adaptive management techniques will be needed to reduce the regeneration of invasive alien species and promote the regeneration of native species in the clear-cut.

Keywords (5-8 words): clear-cut, Hawai‘i, invasive species, seed dispersal

Implications (<120 words; 2-5 bullet points)

- Clear-cutting the invasive tree, *Psidium cattleyanum*, reduced both cover and seed rain of *P. cattleyanum,* but two invasive understory species, *Clidemia hirta* and *Rubus rosifolius*, are the most successful species in the three-year-old clear-cut.
- Long-term, adaptive management will necessary to reduce alien invasive alien cover and facilitate native regeneration in the clear-cut.

Introduction

Islands are global hotspots for endemism and are disproportionately affected by biodiversity loss and habitat degradation compared to continents (Myers et al. 2000; Kier et al. 2009). Invasive alien plant species are major drivers of ecosystem degradation on islands, altering both ecosystem structure and function (Vitousek & Walker 1989; Asner & Vitousek 2005; Sax & Gaines 2008; Kueffer et al. 2010a). Control of invasive species is a critical component of ecological restoration on islands; however, given the large numbers of naturalized alien species and the extinction of many natives, complete restoration of many island ecosystems is impossible (Mascaro et al. 2008; Hobbs et al. 2009; Medeiros et al. 2014; Meyer et al. 2015). In Hawai‘i, many forest restoration projects are “rehabilitation” projects, and the main goal of practitioners is to enrich existing degraded native forests (Friday et al. 2015). Forest patches are selected based on a variety of criteria (e.g., biodiversity, land use history, habitat), fenced to exclude invasive alien ungulates, and treated to reduce aggressive invasive alien species, while native plants are outplanted (*e.g.*, Cabin et al. 2000; Cole et al. 2012; Friday et al. 2015).

Psidium cattleyanum is an invasive tree naturalized on numerous tropical islands, including the Hawaiian Islands (Lowe 2000; Florens et al. 2017). It often grows in dense monocultures, reproducing both clonally and via large quantities of animal-dispersed seeds (Huenneke & Vitousek 1990). Monocultures of *P. cattleyanum* significantly alter overall forest

structure and function, changing forest hydrology (Mair and Fares 2010; Safeeq and Fares 2012; Takahashi et al. 2011), altering litter decomposition (Enoki & Drake 2017), and decreasing native regeneration (Woodward & Quinn 2011). Dense monocultures of *P. cattleyanum* pose a significant challenge for land managers because, once established, removal is difficult, time intensive, expensive, and few removal methods result in increased native cover (OANRP 2010; Woodward & Quinn 2011; Meyer et al. 2019).

Around the world, research and management strategies are increasingly incorporating the theory of secondary succession into ecosystem-based management and restoration techniques (Schliemann & Bockheim 2011). Human-made canopy disturbance, such as removing a stand of invasive species, is one method of trying to initiate native regeneration (e.g., Totland et al. 2005; Tanaka et al. 2010; Heinrichs et al. 2016). But, predicting the trajectories of secondary succession in forests is difficult, and influenced by factors such as land-use history, disturbance severity, and proximity of native and alien propagule sources (Guariguata & Ostertag 2000). Wind-dispersed seeds and small-seeded, animal-dispersed pioneer seeds have enhanced recruitment during secondary succession following a canopy disturbance (e.g., Augspurger 1984, Levey 1988; Schupp et al. 1989, Corlett 1995). Invasive alien species are small-seeded and considered to have enhanced dispersal and establishment outside their native ranges (*e.g.,* Shiels 2011, Jordaan et al. 2011). Large canopy disturbances may facilitate either alien or native regeneration. In the Ogasawara Islands, clear-cutting invasive alien *Bischofia javanica* stands increased native tree regeneration (Tanaka et al. 2010); however, clear-cutting in other tropical systems has led to increased alien regeneration (Totland et al. 2005; Heinrichs et al. 2016). In Hawai‘i, both clear-cutting and gradual removal of an invasive tree, *Morella faya,* promoted a greater regeneration of short-lived alien species than natives (Loh & Daehler 2008).

Many native Hawaiian species do not create persistent soil seed banks (Drake 1998); thus, to achieve native plant regeneration in a clear-cut, native seeds need to disperse into the area. *Metrosideros polymorpha*, a native, wind-dispersed species, is the dominant early succession and mature forest tree in Hawai‘i (Mueller-Dombois & Fosberg 1998; Drake & Mueller-Dombois 1993). Thus, *M. polymorpha* should be an important species regenerating in a clear-cut. However, many other native Hawaiian forest plants are fleshy-fruited and rely on animals for dispersal (Wagner et al. 1999; Sakai et al. 2002). Native seed dispersers are extinct on O‘ahu, and native plants rely on alien songbirds, which are important dispersers for small-seeded native species, though they most commonly disperse alien seeds (Vizentin-Bugoni 2019; Hruska & Drake, *in prep*). Alien dispersers would be critical for small-seeded, fleshy-fruited native species to regenerate in a clear-cut; however, they likely promote alien species.

To understand whether clear-cutting a monoculture of *P. cattleyanum* facilitates native regeneration, I compared patterns of seed rain, seed dispersal, and regeneration in a native-dominated forest and an adjacent three-year-old clear-cut of a monoculture of *Psidium cattleyanum.* Specifically, I asked: are *Metrosideros polymorpha* and small-seeded, animal-dispersed seeds dispersing into the clear-cut? Does the seed rain of fleshy-fruited native and alien species differ between the clear-cut and the surrounding, relatively intact forest? If so, how? What species have regenerated in the clear-cut? I predicted that as a wind-dispersed species, *Metrosideros polymorpha* would be the most abundant native seed in the seed rain both in the forest and in the clear-cut, but that *M. polymorpha* would likely not be recruiting into the clear-cut, owing to a lack of suitable microsites for germination and establishment. I predicted fleshy-fruited alien seeds would be more abundant than native seeds in both the forest and clear-cut, and

that those alien species would be recruiting in the clear-cut more rapidly than were native species.

Methods

Study Site

The Army Natural Resources Program (ANRP) is responsible for managing the forest at Kahanahāiki, a 36-ha management unit in the northern Waiʻanae Mountains (21°32'12.55"N, 158°11'35.40"W). The vegetation at 660 m a.s.l. is mesic forest, receiving approximately 1350 mm of rainfall/year (Giambelluca et al. 2013). The intact forest is a diverse mix of alien and native species, with *Metrosideros polymorpha* as the most abundant canopy species. Native *Acacia koa* and alien *Psidium cattleyanum* and *Schinus terebinthifolius* are the other abundant canopy species. Many fleshy-fruited native species comprise the forest midstory and understory (Appendix 1).

Between 2010 and 2012, OANRP clear-cut a 0.9 ha of *P. cattleyanum* in Kahanahāiki creating a large canopy gap and leaving a few native trees (OANRP 2016). Native trees within the clear-cut included: *Acacia koa* (absolute canopy cover: 16%), *Metrosideros polymoprha* (2.5%), and a few native fleshy-fruited species (Table 1). Large slash piles were broken down using a woodchipper, leaving debris in localized piles. This work was conducted primarily in a 0.5 ha area that was clear-cut in 2012. Between 2010-2016, periodic control of invasive species occurred (OANRP 2016).

Seed Diversity, Abundance, and Dispersal

Seed traps captured seed rain in the forest and 2012 clear-cut area. Traps were constructed from plastic 24.5-cm-diameter pots covered with poultry wire with 2.5 cm hexagonal openings to limit animal access to fruits and seeds within the traps (Drake 1998). Forty traps were placed along 11 transects within the clear-cut (all at least 10 m away from the forest edge), and 108 were placed along management trails within the adjacent forest (Figure 1). Traps were approximately 10 m apart from each other. Samples were collected approximately every four to eight weeks from September 2015-October 2016, then dried and identified to genus and/or species under a dissecting microscope. *Metrosideros polymorpha* seeds were counted if they contained an embryo (Drake 1992). Seeds from fleshy-fruited species were categorized as being within whole or partial fruit, or outside of fruits. For whole fruits with multiple seeds, seed abundance was estimated using either a mean number of seeds/fruit based on field collections or data provided by Wagner et al. (1999) (Appendix 1). As a proxy for seed dispersal, seeds outside of fruit were categorized as "animal-handled" or "not animal-handled." Seeds were classified as animal-handled if they were either in animal feces or found in a sample without whole or partial fruits. By not including seeds outside of fruit—but within a sample with whole or partial fruits of that species—I am likely neglecting the possibility of seeds moved between conspecific fruiting individuals and making a more conservative estimate of bird-mediated dispersal across the landscape.

Vegetation Sampling

Species cover was measured along the seed trap transects within the forest and clear-cut using point-intercept methods (Mueller-Dombois and Ellenberg 1974). Every meter along the transects, cover was measured in three strata: understory (0-2 m), midstory (>2-4 m), and canopy (>4). The under- and midstory were assessed using a 1.3-cm-diameter pole, and the canopy with

a moosehorn densitometer. Species were counted only once within a stratum, even if multiple individuals were intercepted. In total, 218 points were taken in the clear-cut and 388 points in the forest. Species in the understory of the clear-cut were considered to have regenerated in the clear-cut. I did not distinguish whether regeneration was from root sprouts, the seed bank, or dispersal. Midstory and canopy species in the clear-cut are considered to be remnant vegetation. Vegetation surveys were completed from Summer 2016 to Summer 2017.

Analysis

A generalized linear mixed model (GLMM) was used to investigate whether animal-handled seed rain of fleshy-fruited species differed between the clear-cut and the forest for species with sufficient seed rain to allow for statistical comparisons. Fixed model parameters included the location of traps (clear-cut/forest), species, and whether the seeds were animal-handled (Y/N). Sampling date was included as a random factor, and an offset was used to account for the different sampling area in the clear-cut and forest. A poisson distribution was initially used, but data were overdispersed. A "genpois" distribution in glmmTMB was used to account for overdispersion in the data. Analyses were conducted using glmmTMB, car, and DHARMa packages in R 3.6.0 (R Core Team 2019).

Results

Metrosideros polymorpha *seed rain*

Total annual seed rain for *M. polymorpha* was 1,111 +/ 2,307 SD seeds/m^2 in the forest and 387.9 +/- 646 SD seeds/m^2 in the clear-cut. Fewer seeds of *M. polymorpha* were produced in the forest and clear-cut than would be expected given the cover of vegetation (Figure 2). Eighty-eight percent and 85% of traps captured *M. polymorpha* seeds in the forest and clear-cut,

respectively. Seventy-three percent and 93% of *M. polymorpha* seeds were captured in the forest and clear-cut, respectively, from December to March.

Total fleshy-fruited seed rain

Seed traps in the forest captured 28,996 +/- 68,326 SD seeds/m^2/yr, representing five alien and nine native species (Table 1). In the clear-cut, traps captured 67,357 +/- 94,365 SD seeds/m^2/yr, representing five alien and seven native species (Table 1). Two alien species made up over 99% of the seed rain in both the forest and clear-cut: *Clidemia hirta* (forest: 92.3%, clear-cut: 77.3%) and *Rubus rosifolius* (forest: 3.9%, clear-cut: 22.2%). *Clidemia hirta* and *Rubus rosifolius* produced more seeds than would be predicted based on the proportion of cover in the vegetation and other alien and native species produced fewer seeds (Figure 2). *Psidium cattleyanum* seed rain was 29 times more abundant in the forest compared to the clear-cut (Table 1). The most abundant native seeds were *Kadua affinis* (0.06%), *Alyxia stellata* (0.02%), and *Wikstroemia oahuensis* (0.02%) in the forest, and *Dianella sandwicensis* (0.3%), *Psychotria mariniana* (0.01%), and *Kadua affinis* (0.009%) in the clear-cut. In the forest, species in the vegetation but not in the seed rain included *Coprosma foliosa*, *Diospyros sandwicensis, Nestegis sandwicensis* and *Myrsine lessertiana*. In the clear-cut, species in the vegetation but not in the seed rain were *Coprosma foliosa*, *Diospyros sandwicensis, Nestegis sandwicensis,* and *Wikstroemia oahuensis*.

Animal-handled fleshy-fruited seed rain

In the forest, traps captured 6,065 ± 7,094 SD animal-handled seeds/m^2/yr (21% of annual seed rain), representing seven alien and one native species (Table 1). Seeds were almost entirely alien (99.98% of animal-handled seeds). The most abundant species were *Clidemia hirta* (85.9%) and *R. rosifolius* (13.5%). Approximately 20% of all *C. hirta* seeds and 62% of *R.*

rosifolius seeds captured were animal-handled. *Kadua affinis* (0.02%) was the only native species.

In the clear-cut, traps captured 6,589 ± 7,592SD animal-handled seeds/m^2/yr (9.8% of annual seed rain), representing five alien and six native species. Alien seeds were more abundant than natives (99.6% total animal-handled seeds), with *C. hirta* (64.9%) and *R. rosifolius* (34.0%) as the most abundant animal-handled species. Approximately 8% and 15% of *C. hirta* and *R. rosifolius* seeds captured were animal-handled, respectively (Table 1). The most abundant native species was *Dianella sandwicensis* (0.3%).

The proportion of animal-handled seeds was greater for native than for alien species, but the proportions were similar when *C. hirta* and *R. rosifolius* were excluded (Figure 3). Alien species with >35% of seeds handled by animals included: *Passiflora suberosa*, *Psidium cattleyanum*, and *Schinus terebinthifolius* (Table 1). Native species with >35% of seeds handled by animals were captured only as animal-handled seeds and included: *Dianella sandwicensis*, *Psydrax odorata*, and *Scaevola gaudichaudiana*.

Greater than 90% traps captured two or more animal-handled alien species. Ninety-one percent to 100 percent of traps in the clear-cut and forest captured animal-handled *C. hirta* and *R. rosifolius*. In contrast, seeds of *C. hirta* and *R. rosifolius* not handled by animals were in less than 50% of traps. Animal-handed native species were captured by less than 10% of traps in both the clear-cut and the forest.

Five alien species were captured in high enough abundances to statistically test whether the amount of animal-handled seed rain differed between the clear-cut and the forest (*Clidemia hirta, Passiflora suberosa, Psidium cattleyanum, Rubus rosifolius, Schinus terebinthifolius*). The

number of animal-handled seeds varied between the clear-cut and gap, depending on species (GLMM: χ^2= 38.1530; p = <0.001; Figure 4).

Vegetation

Metrosideros polymorpha was the most abundant species in the forest canopy (28% absolute cover), but covered only 2.3% in the mid-story and canopy in the clear-cut (Figure 5). *Metrosideros polymorpha* was not abundant in the forest understory and not recorded in the understory of the clear-cut (Figure 5).

Seven alien and nine native fleshy-fruited species were recorded in the forest. Native species were 30% more abundant than aliens in the understory, but aliens were three times more abundant than natives in the canopy (Figure 5). The most abundant native species in the forest were *Alyxia stellata* and *Coprosma foliosa* (Table 1). *Alyxia stellata* was the only native species that made up >5% of the absolute cover in any stratum in the clear-cut (Table 1). The most abundant alien species in the understory was *Clidemia hirta* and in the canopy were *Psidium cattleyanum* and *Schinus terebinthifolius* (Table 1).

Six alien and seven native fleshy-fruited species were in the clear-cut. Alien species were four times more abundant than natives in the understory (Figure 5). The most abundant alien species in the understory were *C. hirta* and *R. rosifolius* (Table 1). *Clidemia hirta* was approximately equally abundant in the clear-cut and forest understory, but *Rubus rosifolius* was 60 times more abundant in the gap than in the forest. Existing native trees were the most abundant cover in the mid-story and canopy and included native fleshy-fruited species *Psydrax odorata* and *Psychotria mariniana*, wind-dispersed *Metrosideros polymorpha*, (Table 1).

Discussion

Clear-cutting reduced *Psidium cattleyanum* cover and seed abundance (Table 1); however, two invasive understory species are flourishing three years after the clear-cut. *Clidemia hirta* and *Rubus rosifolius* were the most abundant seeds in the overall seed rain and dispersed seed rain, reached 90-100% of all traps, and dominated the plant cover in the clear-cut. Seed production for both *C. hirta* and *R. rosifolius* was higher in the clear-cut than in the forest; however, cover and animal-handled fruits varied for each species. *Clidemia hirta* seed cover was similar in both environments, but seed production in the clear-cut was approximately double that of the forest. *Rubus rosifolius* was 60 times more abundant in the clear-cut than in the forest and had a higher seed abundance in the clear-cut, but had a higher proportion of animal-handled seeds in the forest compared to the clear-cut.

The high abundance of *C. hirta* in both the forest and the clear-cut is not entirely unexpected as it is a prolific invader of disturbed habitats on various islands worldwide, including the Hawaiian Islands (Smith 1992, DeWalt et al. 2004a; DeWalt et al. 2004b). Growth and reproduction of *C. hirta* are more prolific in Hawai‘i compared to its native range (DeWalt et al. 2004a; DeWalt et al. 2004b), and it is a large component of many alien bird diets on O‘ahu (Vizentin-Bugoni 2019). However, the large abundance of seeds and ability to reach most microsites suggests that management of *Clidemia hirta* will be an ongoing endeavor.

Rubus rosifolius is moderately shade-intolerant (PIER 2010), and thus likely more abundant in the clear-cut vegetation compared to the forest owing to the greater light availability. The greater abundance of *R. rosifolius* seeds in the clear-cut may be the result of a greater cover, light-availability, or both, but the high seed production in the clear-cut and high proportion of animal-handled seeds in the forest suggests that it may act as a source for *R. rosifolius* seeds

arriving in the forest. *Rubus rosifolius* makes a persistent seed bank in Hawai‘i (Drake 1998). Although my research does not address the origins of the *R. rosifolius* in the clear-cut, the high proportion of animal-dispersed seeds in the forest and sizable percentage of traps that captured animal-handled *R. rosifolius* both at this site and elsewhere on O‘ahu (Hruska and Drake *in prep*), suggests that *R. rosifolius* will likely be one of the early recruits following canopy disturbances.

Excluding *C. hirta* and *R. rosifolius,* similar proportions of available alien and native seeds were being handled by animals in the clear-cut compared to the forest, but alien seeds were more abundant than native seeds in both environments. Canopy gaps may experience increased seed rain of small-seeded animal-dispersed species owing to larger fruit crops and increased frugivorous bird activity compared to forests (Levey 1998; Wenny and Levey 1998; Wenny 2001). The high fruit production of *Clidemia hirta* and *Rubus rosifolius* in the clear-cut likely attracted birds into the clear-cut. Existing perch trees in gaps also attract frugivorous birds and facilitate the arrival of bird-dispersed seeds, resulting in non-random dispersal patterns (e.g., Schupp et al. 1989; Ferguson and Drake 1999; Shiels and Walker 2003; Guidetti et al. 2016). In a dry forest on Maui, where trees made up approximately 15% of the of the woody plant cover, alien birds deposited more than 96% of all seeds below perch trees (Chimera and Drake 2010). In the clear-cut area, existing native shrubs and trees in the mid-story and canopy are likely foci for seed arrival, but most animal-handled seeds are alien. Furthermore, two of the three alien species with a high proportion of seeds dispersed into the clear-cut were two alien canopy species, *Psidium cattleyanum* and *Schinus terebinthifolius* (Appendix 1). Both species are fast-growing and tolerant of disturbances (Ewe et al. 2003; Uowolo and Denslow 2008). If not

monitored and regularly removed, both species will likely create an alien canopy before native species can recruit into the gap.

Native species are likely recruitment-limited compared to alien species in both the forest and clear-cut (Denslow et al. 2006; Loh and Daehler 2008; Inman-Narahari 2013). Wind-dispersed *Metrosideros polymorpha* was the most abundant native forest canopy tree and the most abundant native seed in the forest and clear-cut. However, seedlings and saplings were not common in the forest or clear-cut understory, suggesting it may be establishment limited. Our methods of vegetation sampling were coarse and *Metrosideros polymorpha* is also a slow growing species, with seedlings growing only a few centimeters per year (Burton and Mueller Dombois 1984), so it is likely that I did not capture *M. polymorpha* seedlings as a result. However, *Metrosideros polymorpha* has also been reported to have lower recruitment in closed-canopy mature forests and higher recruitment in higher light environments, such as lava flows and in canopy gaps (Burton and Mueller-Dombois 1984; Drake and Mueller-Dombois 1993), and higher establishment in microsites that are not bare soil, such as the cracks of lava flows, rock mats, tree ferns, and mossy logs (Drake 1992; Santiago 2000; Inman-Narahari 2013). Since debris in the clear-cut was chipped, a lack of appropriate microsites may contribute to low recruitment of *M. polymorpha* in the understory, despite seeds are arriving there.

Traps in both environments did not capture seeds of many relatively abundant native fleshy-fruited species in the vegetation, suggesting a failure either to produce or disperse seeds (Muller-Landau et al. 2002). Small-seeded species abundant in the vegetation of the forest or clear-cut, but not captured by traps included *Coprosma foliosa* and *Wikstroemia oahuensis.* Seed limitation and dispersal limitation of many fleshy-fruited Hawaiian species is an increasing concern, particularly for restoration efforts (*e.g.*, Denslow et al. 2006; Loh and Daehler 2008;

Inman-Narahari et al. 2013). Additionally, while larger-seeded species (*e.g.*, *Diospyros sandwicensis* and *Nestegis sandwicensis*) were not predicted to be captured in the clear-cut, they also were not captured in the forest. This is not unexpected as their seeds are too large for dispersal by the alien songbirds, likely contributing to recruitment failure (Vizentin-Bugoni 2019; Hruska and Drake *in prep*).

Native Hawaiian plants are reputed to be poor competitors against invasive alien species, particularly in disturbed sites (*e.g.*, Cabin et al. 2002a; Cabin et al. 2002b; Loh and Daehler 2008; Cordell et al. 2009; Thaxton et al. 2012). Most Hawaiian plants have slower growth rates (Pattison et al. 1998; Baruch and Goldstein 1999; Denslow 2003) and are often seed and establishment limited compared to alien species (Loh and Daehler 2008; Cordell et al. 2009; Inman-Narahari 2013). This research supports clear-cutting as a successful strategy for reducing cover of invasive canopy species, but that understory invasive alien species are likely to be an ongoing challenge and potential barrier to native recruitment in the clear-cut. Research following the long-term trajectories of restoration in Hawai‘i suggests that short-term successes do not reflect long-term ecosystem prognosis and that adaptive management and novel strategies, including tolerating and potentially incorporating non-invasive alien species, will be necessary to maintain biodiversity and ecosystem function in Hawaii (Cordell et al 2016).

Tables

Species	Family	Gap % Cover	Gap Total Annual Seed Rain (mean seeds·m^{-2} ± SD)	Gap Animal-handled (mean seeds·m^{-2} ± SD)	Forest % Cover	Forest Total Annual Seed Rain (mean seeds·m^{-2} ± SD)	Forest Animal-handled (mean seeds·m^{-2} ± SD)
Alien							
Clidemia hirta	Melastomataceae	19.7	52056 +/- 94918	4281 +/- 6084	21.1	26752 +/- 70438	5208 +/- 6630
Lantana camara	Verbenaceae	2.3	0.0	0.0	1	0.0	0.0
Passiflora edulis	Passifloraceae	0	0.0	0.0	0.8	0.4 +/- 4.3	0.4 +/- 4.3
Passiflora suberosa	Passifloraceae	3.7	20.4 +/- 102.8	4.5 +- 18.3	1.8	3.3 +/- 23.9	2.3 +/- 21.5
Psidium cattleyanum	Myrtaceae	1.8	27.6 +/- 111.7	10.2 +/- 15.9	12.1	810.1 +/- 2409	22.9 +/- 57.8
Psidium guajava	Myrtaceae	0	0.0	0.0	0	0.2 +/- 2.1	0.2 +/- 2.1
Rubus rosifolius	Rosaceae	49.1	14954 +/- 23910	2238 +/- 3415	0.8	1331 +/- 4187	825 +/- 1751
Schinus terebinthifolius	Anacardiaceae	0.9	25.0 +/- 90.5	25.0 +/- 90.5	8.5	103.2 +/- 321.5	5.3 +/-15.8
Total		--	67082	6562	--	29000	6064
Native							
Alyxia stellata	Apocynaceae	9.2	1.7 +/- 7.8	0.0	30.9	5.9 +/- 21.4	0.0
Coprosma foliosa	Rubiaceae	4.6	0.0	0.0	10.6	0.0	0.0
Dianella sandwicensis	Asphodelaceae	0	20.0 +/- 126	20.0 +/- 126	0	0.0	0.0
Diospyros sandwicensis	Ebenaceae	2.3	0.0	0.0	2.1	0.0	0.0
Kadua affinis	Rubiaceae	0	6.1 +/- 35.2	0.6 +/- 3.5	3.1	17.0 +/- 146.8	1.0 +/- 5.6
Leptecophylla tameiameiae	Ericaceae	0	0.6 +/- 3.5	0.0	0	0.0	0.0
Myrsine lessertiana	Primulaceae	0	0.6 +/- 3.5	0.6 +/- 3.5	0.8	0.0	0.0
Nestegis sandwicensis	Oleaceae	1.8	0.0	0.0	1.3	0.0	0.0
Psychotria mariniana	Rubiaceae	0	0.6 +/- 3.5	0.6 +/- 3.5	0	0.0	0.0
Psydrax odorata	Rubiaceae	0.9	2.8 +/- 14.4	2.8 +/- 14.4	3.9	0.6 +/- 4.8	0.0

Scaevola gaudichaudiana	Goodeniaceae	0.9	1.8 +/- 10.5	1.8 +/- 10.5	0.8	0.6 +/- 4.8	0.0
Wikstroemia oahuensis	Thymelaeaceae	0.5	0.0	0.0	1.5	6.6 +/- 44.7	0.0
Total		--	40.2	26.7	--	30.3	1.0

Table 2.1 Fleshy-fruited species recorded in the vegetation and seed rain in the clear-cut and surrounding forest. Percent cover is the absolute cover in the stratum where the species is most reproductive (Appendix 1). Total seed rain includes seeds both inside and outside fruits, including animal-handled seeds. Animal-handled seeds are those found in in samples with bird feces and/or without whole or partial fruits.

Figure

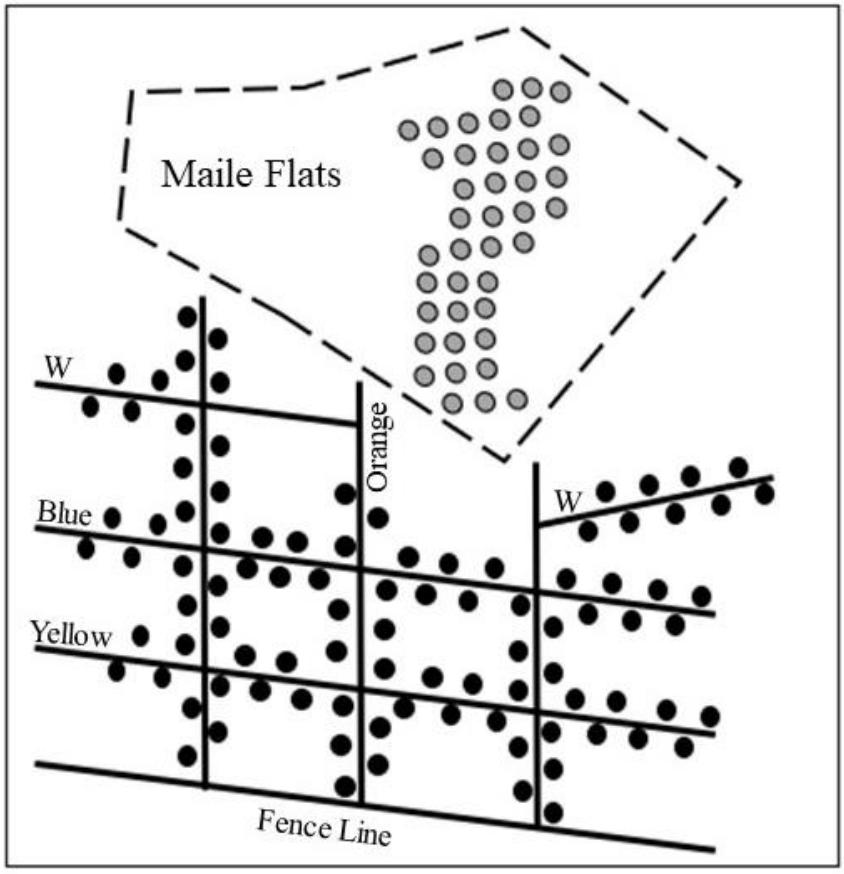


Figure 2.1 Schematic of field site and location of seed rain traps at Kahanahāiki Management Unit (not to scale). One hundred and eight traps were placed along management trails in intact forest of mixed alien and native species. Forty seed rain traps were placed on transects throughout Maile Flats, an area where a monoculture of *Psidium cattleyanum* had been clear-cut and chipped. The dotted polygon represents the approximate boundaries of the 2012 clear cut.

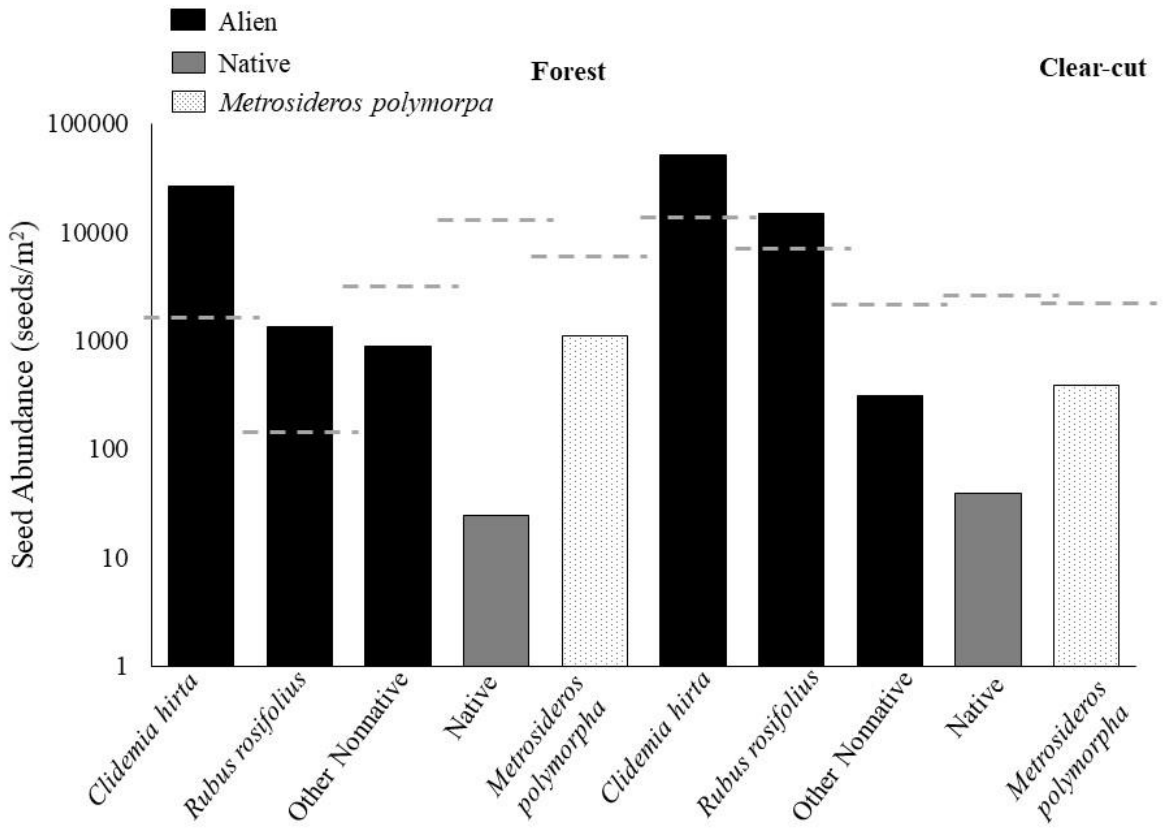


Figure 2.2 The annual seed rain of fleshy-fruited alien and native species and wind-dispersed *Metrosideros polymorpha* compared to percent cover in the vegetation at each site. Annual seed rain is the total number of seeds captured per m^2 and includes seeds found in whole or partial fruit, or outside fruit (including animal-handled seeds) and is presented on a logarithmic scale to compare native (100s of seeds) and alien seeds (1000s of seeds). The dashes line represents the expected annual seed rain of fleshy-fruited species if seed production was proportional the cover of alien and native species in the vegetation. Forest: $\chi^2 = 82314377$, $p < 0.0001$; Clear-cut: $\chi^2 = 176736$, $p = <0.0001$

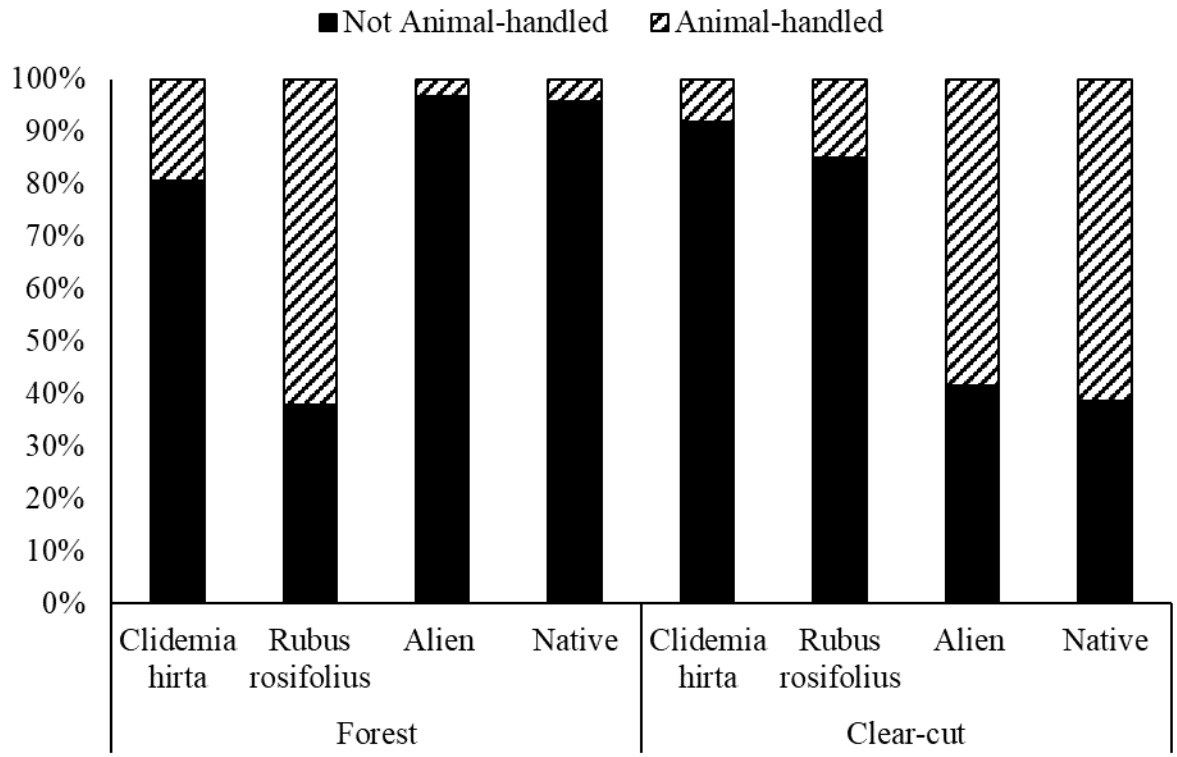


Figure 2.3 The proportion of animal-handled alien and native seed rain in the forest and clear-cut. Alien species *Clidemia hirta* and *Rubus rosifolius* are separated because of their exceptionally large seed production in the forest and clear-cut. Seed rain traps captured five alien species (excluding *C. hirta* and *R. rosifolius*) and one native species in the forest, and three alien species and seven native species in the clear-cut (Table 1).

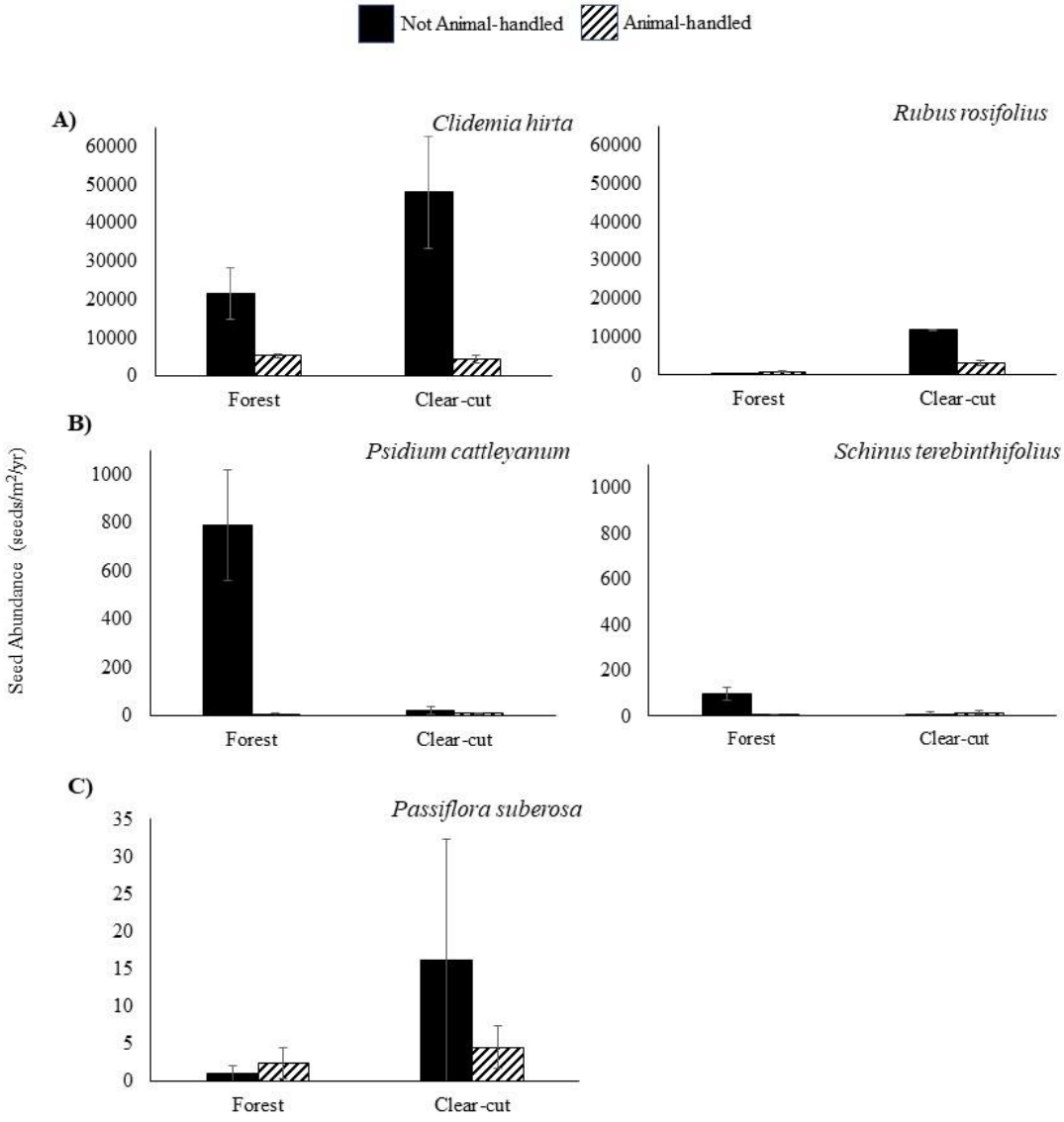


Figure 2.4. Mean annual seed rain (± sem) of the five alien species in the clear-cut and adjacent forest used in GLMM. Animal-handled seed rain did vary between the clear-cut and forest depending on species (χ^2= 38.1530; p = <0.001). A) The seed rain of the two most abundant understory alien species, *Clidemia hirta* and *Psidium cattleyanum.* B) The seed rain of the two most abundant alien canopy species *Psidium cattleyanum* and *Schinus terebinthefolius.* C) The seed rain of understory *Passiflora suberosa*.

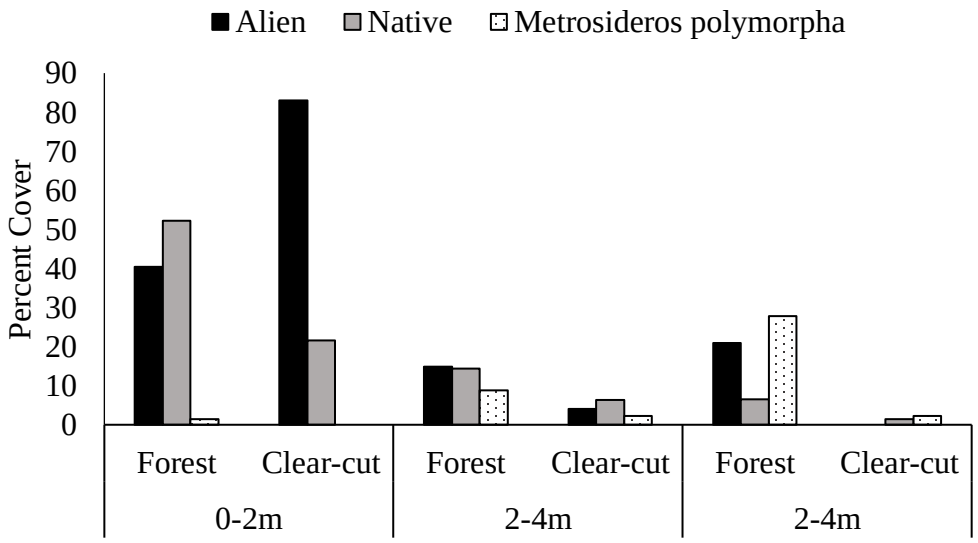


Figure 2.5 The absolute percent cover of alien and native fleshy-fruited species and wind-dispersed *Metrosideros polymorpha* in area cleared of invasive *Psidium cattleyanum* (clear-cut) and surrounding forest in the understory (0-2 m), mid-story (2-4 m), and canopy (>4 m).

Chapter 4: The effect of canopy cover on germination and seedling survival of four Hawaiian forest species

Abstract

Habitat loss and invasive species have irreversibly altered islands. As restoration efforts increase, time- and cost-effective methods are needed to increase native plant recruitment in ecological restoration. Sowing seeds is a potentially effective method for increasing survival, but little is known about how seeds perform under varying field conditions. I investigated the effect of canopy cover on the germination and seedling survival of four common native plant species—*Alyxia stellata, Coprosma foliosa, Dianella sandwicensis,* and *Leptecophylla tameiameiae*—in a mesic forest on O‘ahu, Hawaiian Islands. Germination and survival were monitored for 32-45 weeks, depending on species. *Alyxia stellata* and *Coprosma foliosa* germination had approached its maximum at week 21 and 45, respectively. *Dianella sandwicensis,* and *Leptecophylla tameiameiae* had not approached maximum germination by the end of their study period. Germination of *Alyxia stellata* and *Coprosma foliosa* was positively correlated with canopy cover. Survival of seedlings was positively correlated with canopy cover for *Coprosma foliosa*. Canopy cover could be a useful metric for determining habitat suitability for sowing seeds in forest restoration sites.

Keywords: Hawaii, field germination, canopy cover, *Alyxia stellata, Coprosma foliosa, Dianella sandwicensis, Leptecophylla tameiameiae*

Introduction

Habitat destruction and invasive species have disproportionately affected islands globally, and restoration of these ecosystems is an ongoing endeavor (Towns and Ballantine 1993; Sax and Gaines 2008). Restoration on islands is a process that often involves excluding alien ungulates, removing invasive plant species, and increasing the abundance of native species (*e.g.*, Cabin et al. 2000; Thaxton et al. 2010; Weller et al. 2011). Methods to increase native species include increasing habitat for regeneration and augmenting native populations via seed additions and outplanting (Guerrant and Kaye 2007; Jones 2013). The Hawaiian Islands are the most isolated oceanic islands and are renowned for their biodiversity, and the impacts habitat destruction and invasive species have had on ecosystem structure and function (*e.g.*, Mueller-Dombois & Fosberg 1998; Mack et al. 2001; Rothstein et al. 2004; Asner et al. 2006; Asner et al. 2008; Denslow et al. 2009). Over the past three decades, Hawai‘i has also become a natural laboratory for restoration research, investigating methods of invasive species removal and native species conservation (*e.g.*, Cabin et al. 2000; Cabin et al. 2002a; Cole et al. 2012; Thaxton et al. 2012; Friday et al. 2015; Cordell et al. 2016).

Seeds are becoming increasingly important for ecosystem conservation and restoration because storing and sowing seeds is less expensive and requires less space and time than cultivating and outplanting seedlings and mature individuals (Budelsky and Galatowitsch 1999). In Hawai‘i, both direct and broadcast seeding are increasingly recommended and utilized in restoration efforts (Friday et al. 2015). Direct seeding involves sowing seeds in specific microsites and may involve microsite modification (Grossnickle and Ivetic 2017). Broadcast seeding is where managers disperse seeds throughout a restoration site (Grossnickle and Ivetic 2017). Across islands, germination and survival differ by species, environmental conditions, and

methodology (Cabin et al. 2002; Brooks et al. 2009; Ammondt et al. 2013; Gould et al. 2013). Although data on seed dormancy and germination under controlled conditions exists for numerous Hawaiian species (Baskin and Baskin 2014), information regarding germination and survival of species in the field is limited (Friday et al. 2015).

Over half of the flowering plants in Hawai‘i are fleshy-fruited and adapted for bird dispersal (Sakai et al. 2002; Price and Wagner 2004); however, almost all native seed dispersers are extinct (Atkinson 1977). Across the islands, many fleshy-fruited native plants are seed and dispersal limited, and regeneration of these species across the landscape will likely require intervention beyond invasive species removal (Loh and Daehler 2008; Cordell et al. 2009; Inman-Narahari et al. 2013; Chapter 3). O‘ahu is the most densely populated main Hawaiian Island and has the least remaining forest cover (Cuddihy and Stone 1990). All native seed dispersers are extinct and all alien birds disperse mostly alien plants (Vizentin-Bugoni et al. 2019; Chapter 2). These factors may partially explain why fleshy-fruited native plants are failing to recruit in restoration areas (Whitehead 2016; Chapter 3).

Removing invasive species in restoration sites alters canopy cover and, in turn, affects the germination and survival of both artificially sown and naturally dispersed species (*e.g.,* Cabin et al. 2002b; McAlpine and Drake 2002; Cordell et al. 2009; Thaxton et al. 2012). Canopy cover in forests has been correlated with abiotic factors at the soil surface that affect germination and seedling survival such as light intensity, temperature, wind speed, and relative humidity (e.g., Balisky and Burton 1995; Gonzalez-Rodriguez et al. 2001; Delgado et al. 2007; Boggs and McNulty 2010), and biotic factors like pathogens and disease (Condeso and Meentemeyer 2007; Meetenmeyer et al 2008; Jones 2006). Thus, canopy cover may be useful for predicting suitable microhabitats for native species in restoration sites.

I investigated the effect of canopy cover on the germination and seedling survival of four native fleshy-fruited forest species in a restored forest on Oʻahu: *Alyxia stellata* (J.R. Forst. & G. Forst.) Roem. & Schult. (Apocynaceae), *Coprosma foliosa* A. Gray (Rubiaceae), *Dianella sandwicensis* (Hook. & Arnott (Asphodelaceae), and *Leptecophylla tameiameiae* (Cham. & Schltdl.) C. M. Weiler (Ericaceae). All four are relatively common species that are likely seed and dispersal limited (Chapters 2 and 3), and thus make good candidates for seed sowing or broadcasting to increase native regeneration. All species, except *C. foliosa*, have previously undergone controlled experiments to test seed germination and dormancy behavior (Baskin et al. 2004; Baskin et al. 2005; Baskin and Baskin 2014; Wolkis et al. 2018), but germination and seedling survival have not been experimentally tested in the field.

Methods

Study Site

Kahanahāiki is a 36-ha management unit in the northern Waiʻanae Mountains (21°32'12.55"N, 158°11'35.40"W). At 660 m a.s.l., the site receives approximately 1350 mm of rainfall/year (Giambelluca et al. 2013). The vegetation is mesic forest made up of both native and alien species. Abundant canopy species include natives *Metrosideros polymorpha* Gaud. (Myrtaceae) and *Acacia koa* A. Gray (Fabaceae), and aliens *Psidium cattleyanum* Sabine (Myrtceae) and *Schinus terebinthifolius* Raddi (Anacardiaceae) (Chapter 3). The mid- and understory layers are comprised of many fleshy-fruit native and alien species (Chapter 3).

Study Species

Species selection was based on fruit availability during February - July of 2018. All four species are relatively common in mesic to wet forests on Oʻahu, but some are also widespread in Hawaiʻi and elsewhere in the Pacific. *Alyxia stellata* is an understory liana widespread

throughout Pacific Islands and found in many vegetation types (Wagner et al. 1999). *Coprosma foliosa* (Rubiaceae) is an endemic understory shrub in mesic to wet forest (Wagner et al. 1999). *Dianella sandwicensis* is an endemic perennial herb endemic found in open to partially open sites (Wagner et al. 1999). *Leptecophylla tameiameiae* is an under- to mid-story shrub found in the Hawaiian and Marquesas Islands throughout diverse habitats, including mesic forests, alpine shrubland, and bogs (Wagner et al. 1999). All four species are fleshy-fruited, but differ in seed size and dormancy class (Table 1). Fruits were collected from at least 10 different maternal plants within the site, cleaned of pulp in a laboratory, and the seeds returned to the field within two weeks.

Experimental Setup

Thirty-five points of varying canopy cover (0-100 % cover) were selected to test how canopy cover affects germination (Figure 1). Cover was measured using a spherical densiometer (Lemon 1956). At each point, each species was sown flush with the ground in three 2.5 cm diameter PVC pipes (= subplots), each 3 cm long. Pipes were positioned in the ground to have a 5 mm rim above the soil surface and contained soil that had been sieved to remove large debris and reduce compaction. Hardwire mesh (6 mm x 6 mm) covered the pipes to reduce seed and seedling depredation. The number of seeds per PVC pipe varied by species due to seed size???: *C. foliosa* = 3 seeds/pipe, *A. stellata* = 1 seed/pipe, *D. sandwicensis* = 5 seeds/pipe, *L. tameiameiae* = 1 drupe/pipe. *Leptecophylla tameiameiae* drupes can contain up to six seeds; but > 99% of drupes contain one to five seeds and drupes can produce a maximum of five seedlings (Baskin et al. 2005). Germination was recorded every 2-8 weeks between 16 April 2018 and 7 May 2019. Germination was noted when cotyledons were exposed.

Analysis

Generalized linear mixed models (GLMMs) tested whether maximum germination and seedling survival depended on canopy cover. Pipe, nested within cover, was included as a random variable. Because there was one seed/subplot for *Alyxia stellata,* and germination was either 0 or 1, a binomial distribution was used. For remaining species where there was a maximum count (= multiple seeds) per subplot, a Poisson distribution was used. Analyses were conducted using packages lme4 and DHARMa in R version 3.6.0.

Results

Alyxia stellata

Germination first occurred 12 weeks after planting. After 39 weeks, 51% of seeds had germinated (Table 2). Percent germination reached an asymptote at around Week 21 (Figure 2). Seeds germination was positively correlated with canopy cover (Figure 3A; $\chi^2 = 5.022$, $p = 0.002$). Of the seeds that did germinate, 47% remained alive at week 39 (Table 2). Canopy cover did not affect the number of seedlings alive at week 39 (Figure 3B; $\chi^2 = 1.607$, $p= 0.205$).

Coprosma foliosa

Germination first occurred 18 weeks after planting. After 45 weeks, 34% of seeds had germinated (Table 2), and germination started to approach an asymptote, though it may still be ongoing (Figure 2). More seeds germinated under areas of greater canopy cover than under lower cover (Figure 4A; $\chi^2 = 5.022$, $p = 0.025$). Of the seeds that germinated, 52% were alive at week 45 (Table 2). Seedling survival was positively correlated with canopy cover (Figure 4B; $\chi^2 = 6.547$; $p = 0.011$).

Dianella sandwicensis

Germination first occurred at week 12. By week 39, 16% of the *Dianella sandwicensis sown* had germinated (Table 2). Whether percent germination reached an asymptote or was still

increasing was unclear (Figure 2). Germination of *Dianella sandwicensis* was independent of canopy cover (Figure 5A; $\chi^2 = 0.233$, $p = 0.630$). After 39 weeks, only 34% of the germinated seeds were still alive (Table 2). Survival of seedlings did not vary under different levels of canopy cover (Figure 5B; $\chi^2 = 0.021$, $p = 0.886$).

Leptecophylla tameiameiae

Germination first occurred at Week 24. At Week 32, two percent of the seeds germinated (Figure 2). Also at Week 32, germination was independent of canopy cover (Figure 6A; $\chi^2 = 0.233$, $p = 0.182$) or seedling survival to Week 32 (Figure 6B; $\chi^2 = 0.007$, $p = 0.935$). Ten percent of the germinated seedlings were alive at Week 32 (Table 2).

Discussion

Few studies have examined seed germination of native Hawaiian species in the field. This research demonstrates that germination and seedling survival under various levels of cover differs among species. *Alyxia stellata* and *Coprosma foliosa* were both positively correlated with canopy cover; however, *Dianella sandwicensis* and *Leptecophylla tameiameiae* germination were not affected by canopy cover. Canopy cover did not affect survival for three species, but survival of *C. foliosa* was positively correlated with canopy cover. Estimates of germination and surviving seedlings were conservative because seeds may have germinated and died between censuses.

Alyxia stellata

Percent germination of *A. stellata* in the field was approximately six times greater and maximum germination occurred in half the time compared to seeds germinated under controlled conditions (Baskin et al. 2004, Table 1). A positive correlation between germination and canopy cover was slightly unexpected as *A. stellata* is common throughout many vegetation types,

including open habitats (Wagner et al. 1999). *Alyxia stellata* seeds were the largest seeds tested in this study (Table 1). Large seeds have been reputed to perform better in shaded environments compared to open environments (Fenner and Thompson 2005). It is possible that temperatures were either too high or there was not enough moisture for *A. stellata* seeds in more open environments (Foster 1986; Everham et al. 1996)

Coprosma foliosa

Germination information under controlled conditions was not available specifically for *C. foliosa*, so predicted seed behavior was based on controlled experiments with other Hawaiian *Coprosma* species (Baskin et al. 2004; Table 1). In the field, first germination of *C. foliosa* occurred later compared to other Hawaiian species in controlled environments (Baskin et al. 2004). Under controlled conditions, *Coprosma* species also had 50% or more seeds germinate within 5-8 weeks after planting (Baskin et al. 2004; Table 1). In New Zealand, four species of *Coprosma* first germinated after 2.5 to 16 weeks, reached maximum germination at 10 to 31 weeks, and had >90% germination in controlled conditions (Burrows 1995; 1996a; 1996b; 1996c).

Both germination and seedling survival were positively correlated with canopy cover. *Coprosma foliosa* is found primarily in forest habitats and may be restricted to forests because of specific germination requirements correlated with canopy cover. *Coprosma foliosa* was the only species with cover-dependent survival. Seedlings did experience herbivory, but some seedlings were also noted to have a possible pathogen on their leaves (*personal observation*). Pathogens may be correlated with canopy cover or species directly above the seedlings (Augspurger and Kelly 1984; Augspurger 1984; Chacón and Armesto 2005; Álvarez-Loayza et al. 2011; Goodale et al. 2014).

Dianella sandwicensis and *Leptecophylla tameiameiae*

Germination of *D. sandwicensis* and *L. tameiameiae* was still occurring at week 39 and 32, respectively. Under controlled conditions, germination of *D. sandwicensis* can take up to 106 weeks to reach maximum germination and *L. tameiameiae* can take up to 162 weeks (Baskin et al. 2005; Wolkis et al. 2018). Additionally, both *D. sandwicensis* and *L. tameiameiae* can have >50% germination under controlled conditions (Wolkis et al. 2018). Because so few *D. sandwicensis* and *L. tameiameiae* seeds germinated within 39 and 32 weeks and both species have long dormancy periods, it is possible that canopy cover may still be an important factor for germination and survival of these species over time.

Implications for Restoration

Seedling mortality for all species was at least 48%. Reasons for mortality were not always evident, but seedling herbivory was observed for all species except *L. tameiameiae* (*personal observation*). All observed depredated seedlings were large enough to be growing through the hardwire cloth. Herbivory of *L. tameiameiae* seedlings may not have been evident as seedlings are small and were not observed growing outside of the hardwire mesh. Evidence of herbivory may not have been noticeable because of their small size or seedlings were protected from herbivory and died from other causes within the pipes, such as pathogens or drought.

Few studies have identified specific causes of seedling mortality in Hawaiian plants (Drake and Pratt 2001; Joe and Daehler 2008). Drake and Pratt (2001) followed 300 artificial seedlings on the forest floor and found that small-scale physical disturbance, such as litterfall or trampling by animals, is an important factor in seedling mortality. Alien herbivores, such as slugs, also contribute to mortality of some native Hawaiian seedlings (Joe and Daehler 2008). Seeds and seedlings for this study were protected from small scale disturbances, but herbivory

was noted for three of the species when they were large enough to grow beyond the hardwire mesh. Sowing seeds in areas not frequently trampled by humans and that exclude alien ungulates likely increases survival (*e.g.* Drake and Pratt 2001; Cabin et al. 2000, Cole et al. 2012). Additionally, control of invasive snails and slugs during expected germination times of sown seeds could also increase germination and survival (Joe and Daehler 2008).

Canopy cover may be a useful predictor for determining where to sow seeds to get the highest percent yield of seedlings in forest restoration for *A. stellata* and *C. foliosa*; however, it is likely too early to determine the effect of canopy cover on *D. sandwicensis* and *L. tameiameiae* (plots of these species are still continuing to be monitored). Both *A. stellata* and *C. foliosa* are common species that are recruitment limited (Whitehead 2016; Chapter 2 and 3). Regeneration would likely benefit from depulping and sowing seeds of in forest.

Tables

Table 3.1 List of species planted in the field and their seed size (longest axis), dormancy class, and estimated time interval for germination under controlled conditions.

Species	Percent Cover	Seed Size (mm)	Class of Dormancy	Time to 50% or maximum % germination (weeks)	Reference
Alyxia stellata	41.1	14	Nondormant/Physiological	40 (8% max. germ.)	Baskin et al. 2004
Coprosma foliosa	15.2	6.7	Physiological*	5-8*	Baskin et al. 2004
Dianella sandwicensis	0	3	Morphophysiological	18-80	Wolkis et al. 2018
Leptecophylla tameiameiae	0	2.4	Deep Physiological	56-162	Baskin et al. 2005

* = species information inferred based on similar seeds in the same family (Baskin and Baskin 2014)

Table 3.2 Experimental duration, germination, and survival as of 7 May 2019.

Species	Date Planted	Total Weeks	Seeds Planted	Total Germination	Survival at Final Count
Alyxia stellata	15-Jul-18	39	105	54	29
Coprosma foliosa	16-Apr-18	45	315	106	56
Dianella sandwicensis	15-Jul-18	39	525	86	29
Leptecophylla tameiameiae	2-Jul-18	32	525 (2625)*	53	28

*For the multi-seeded drupes of *Leptecophylla tameiameiae*, the number in the parentheses is the number of seeds planted assuming each drupe contains five seeds.

Figures

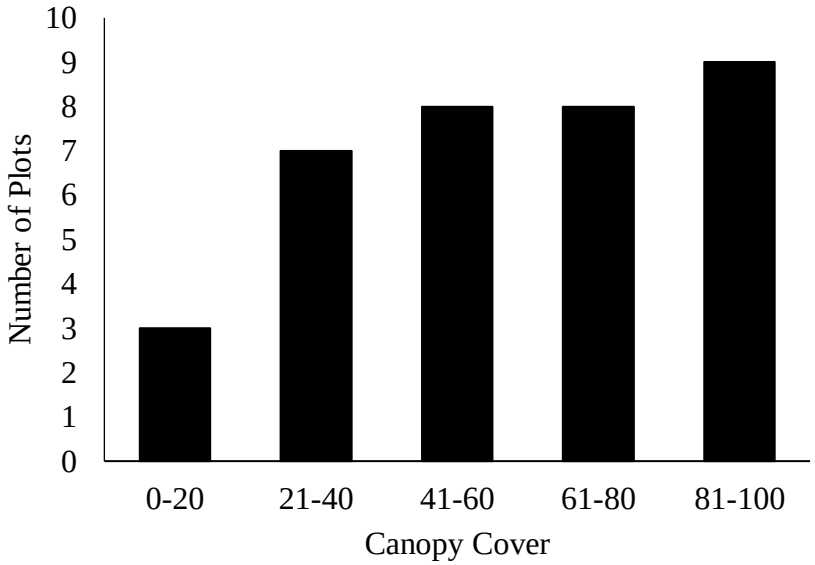


Figure 3.1 The frequency distribution of the canopy cover (%) for the germination plots.

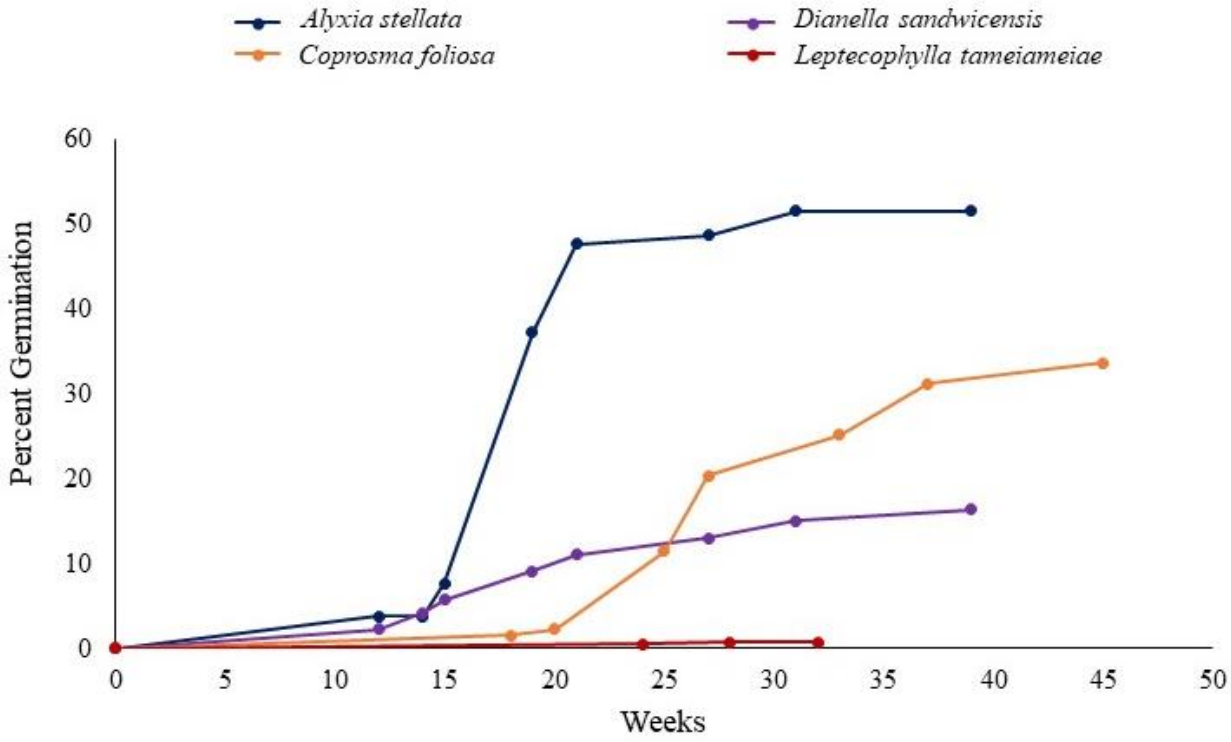


Figure 3.2 The percent germination across all canopy cover levels through time for each species. Each species were planted on different dates (Table 2), but have been adjusted to compare germination rates in one figure.

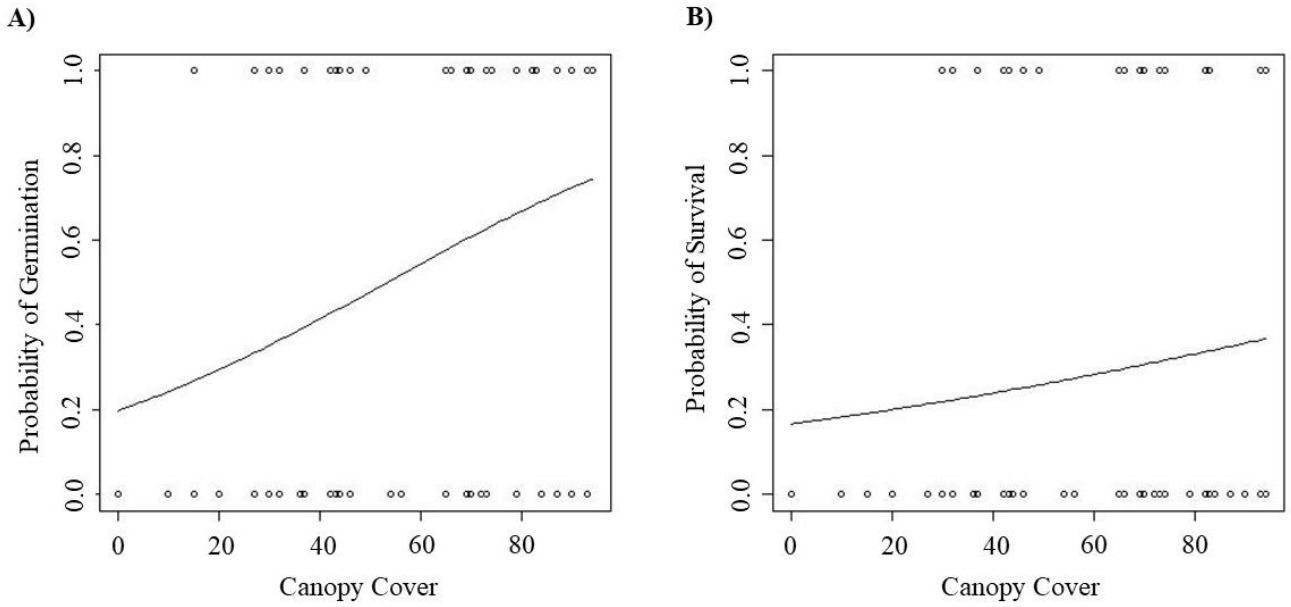


Figure 3.3 The probability of *Alyxia stellata* seeds **A)** germinating and **B)** surviving under varying levels of canopy cover (%) after 39 Weeks. Points represent germination and survival per subplot.

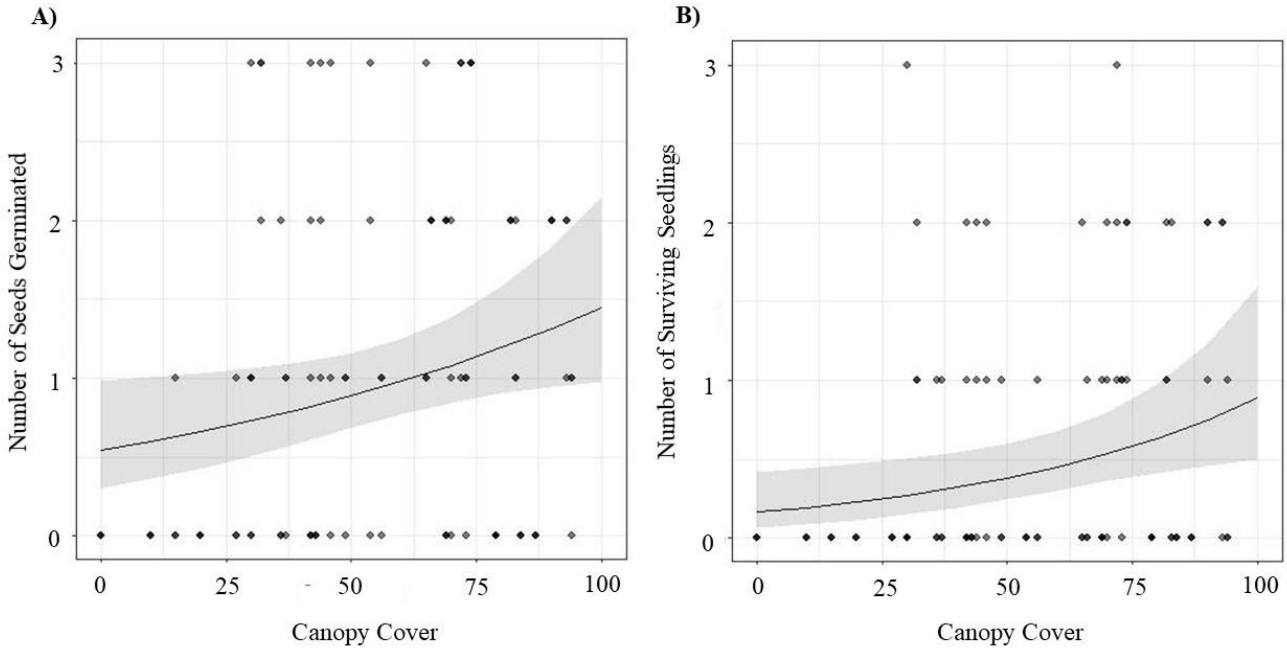


Figure 3.4 The relationship between canopy cover and **A)** the total number of seeds germinated (maximum = 3) and **B)** the total number of seedlings to survive at week 45 for *Coprosma foliosa* (with 95% confidence intervals). Points represent germination and survival per subplot.

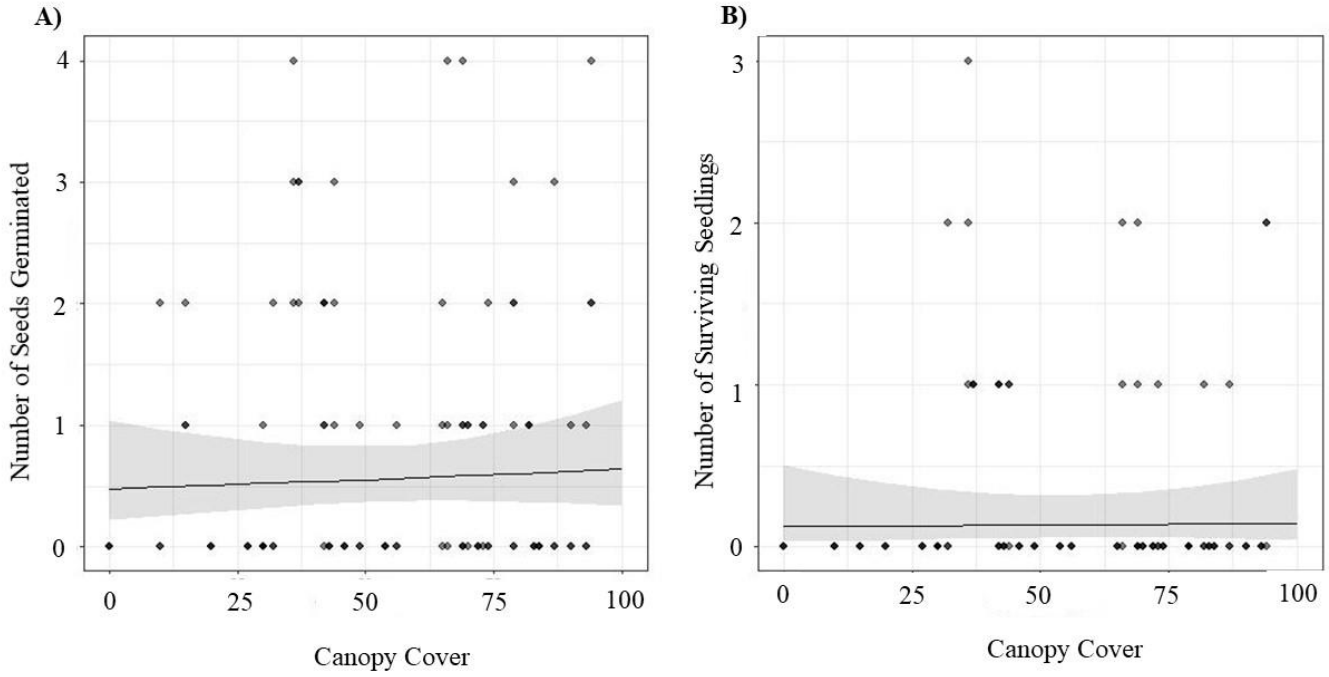


Figure 3.5 The relationship between canopy cover and **A)** the total number of seeds germinated (maximum = 5) and **B)** the total number of seedlings to survive at Week 39 for *Dianella sandwicensis* (with 95% confidence intervals). Points represent germination and survival per pipe.

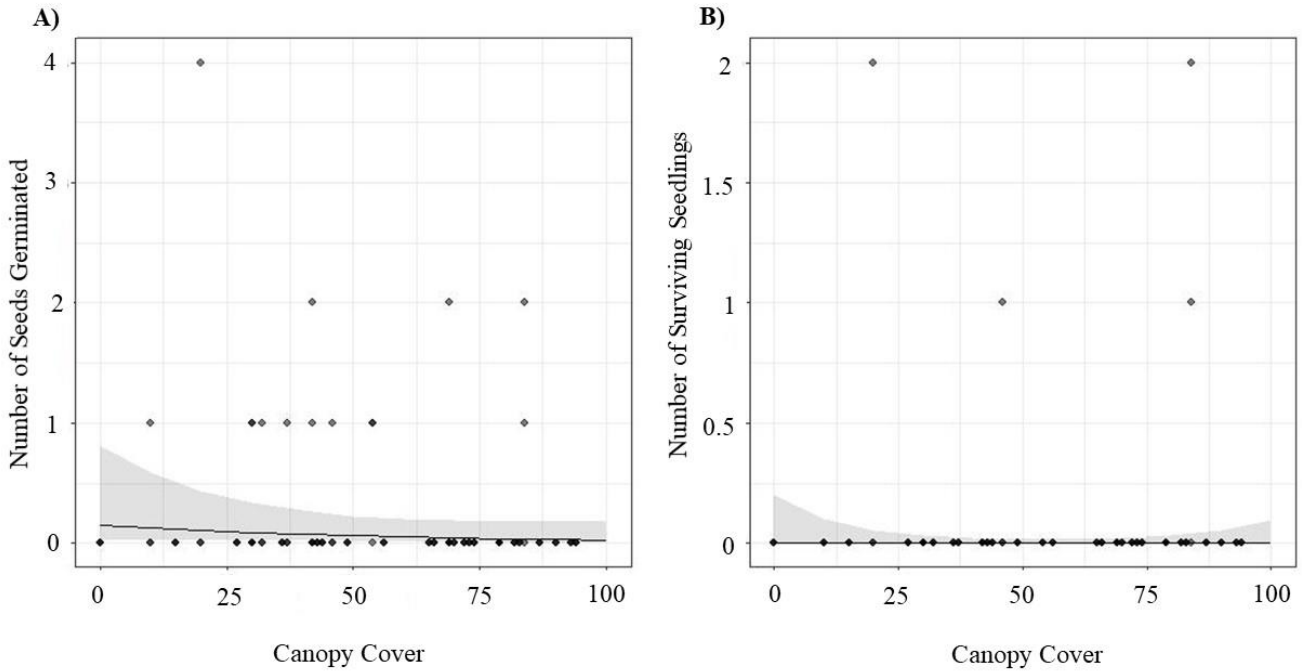


Figure 3.6 The relationship between canopy cover and **A)** the total number of seeds germinated (maximum = 25) and **B)** the total number of seedlings to survive at Week 32 for *Leptecophylla tameiameiae* (with 95% confidence intervals). Points represent germination and survival per pipe.

Chapter 5: Conclusion

Alien birds as seed dispersers

These findings support alien birds as the primary dispersers of small-seeded alien and native species on O‘ahu, leaving large seeded species dispersal limited (Vizentin-Bugoni 2019). Dispersed alien seeds were more abundant compared to dispersed native seeds and represented some of the most important tropical invaders globally (Daehler et al. 2004; Lowe et al. 2000). Alien seed dispersal was also captured by seed traps more frequently on the landscape compared to natives. High fruit and seed abundances of aliens compared to natives may partially explain the low frequency of dispersed native seeds on the landscape. Species that produce larger fruit crops of small seeds have a greater probability of being removed by birds at higher rates and deposited into more seed traps (Howe and Estabrook 1977; Izhaki 2002).

Invasive alien seeds dispersed into more seed traps compared to native seeds, suggesting that propagule pressure is likely an important component of invasion success in O‘ahu forests, particularly for *Clidemia hirta* (Melastomaceae) and *Rubus rosifolius* (Rosaceae) (Lockwood et al. 2005; Simberloff 2009). At Mount Ka‘ala (MTK), where alien cover was <5%, approximately half of the seed traps captured dispersed invasive seeds. The high frequency of these dispersed invasive seeds suggests that these plants are either abundant in the areas around MTK, or repeatedly visited and brought into the site by birds (Rose et al. 2017), suggesting that alien birds are responsible for continually introducing invasive seeds into forests where they are otherwise rare. Since alien birds have been found to interact predominantly with alien species on O‘ahu (Vizentin-Bugoni 2019), and I found seeds dispersed into a high percentage of traps at MTK, it is likely that alien birds may be seeking out abundant alien plant species.

Seed dispersal research both in the Hawaiian Islands and on other island systems(?) have found alien birds may contribute to the spread of invasive alien plants on islands. Studies on

Hawai‘i Island and Kaua‘i found that sites with one native and multiple alien bird dispersers had fewer alien and more native species dispersed compared to sites without a native disperser (Pejchar 2015; Kaushik et al. 2018). On Maui, where native dispersers are also extinct, Chimera and Drake (2010) found that alien birds dispersed predominantly alien seeds in dry forests, likely facilitating the spread of invasive species. Alien Red-whiskered bulbuls (*Pycnonotus jocsus*) on Reunion Island, dispersed multiple invasive alien species, including *Schinus terebinthefolius* (Anacardiaceae) and *Lantana camara* (Lamiaceae) (Mandon-Dalger et al. 2004). Alien Red-vented bulbuls (*Pycnonotus cafer*) preferred the fruit of and invasive species compared to another alien and two native species in captivity on the island of Moorea (Spotswood et al. 2013).

Implications for native recruitment

This dissertation supports a larger body of forest and restoration research showing that fleshy-fruited native species are recruitment-limited compared to alien species (Denslow et al. 2006; Loh and Daehler 2008; Inman-Narahari 2013). In Chapters 2 and 3, all native seeds were captured by traps in low abundances, with some common vegetation species not captured. Additionally, only small-seeded natives were potentially dispersed by alien birds into traps. Poor dispersal and infrequent capture rates by traps suggest that fleshy-fruited native species are seed or dispersal limited (Mueller-Landau et al. 2002).

Lack of dispersal could have several negative consequences for native plant species. Seeds that occur at higher densities under parent trees may be subjected to higher levels of depredation (*e.g.*, Wenny 2000; Moles and Drake 1999; Chimera and Drake 2011). Seedlings that occur at high densities below parent plants are likely to experience higher rates of mortality because of density-dependent seedling depredation, competition, or greater exposure to

pathogens from the parent plant (*e.g.*, Augspurger 1984; Moles and Drake 1999; Hansen et al. 2008; Wotton and Kelly 2011). Furthermore, native seeds dispersed by alien birds may be deposited in either favorable or poor microsites, particularly in mixed forests where alien species in the vegetation likely create unfavorable microsites; thus, research investigating deposition environments of native seeds is increasingly important (McConkey et al.2012; Yelenik 2016).

Metrosideros polymorpha (Myrtaceae), a native, wind-dispersed species, is the dominant early succession and mature forest tree in Hawai‘i (Mueller-Dombois and Fosberg 1998; Drake and Mueller-Dombois 1993). In Chapter 3, *M. polymorpha* was the most abundant native forest canopy tree and the most abundant native seed in the forest and clear-cut; however, seedlings and saplings were not common in the understory, supporting other findings that *M. polymorpha* is establishment limited (Denslow et al. 2006; Inman-Narahari 2013). *Metrosideros polymorpha* has been reported to have lower recruitment in closed-canopy mature forests and higher recruitment in higher light environments, such as lava flows and in canopy gaps (Burton and Mueller-Dombois 1984; Drake and Mueller-Dombois 1993), and higher establishment in microsites that are not bare soil, such as the cracks of lava flows, rock mats, tree ferns, and mossy logs (Drake 1992; Santiago 2000; Inman-Narahari 2013). Thus, a lack of appropriate microsites may contribute to low recruitment of *M. polymorpha* in the clear-cut and closed canopy environments, despite seeds are arriving there.

It is unclear if recruitment limitation is a consequence of invasive alien species, or facilitates invasives; it is likely a combination (Didham et al. 2005; MacDougall and Turkington 2005). Invasive alien species may outcompete native species and alter habitats (Vitousek and Walker 1989; Asner and Vitousek 2005; Sax and Gaines 2008; Kueffer et al. 2010), or seed and dispersal limitation may facilitate the decline of native plant populations in Hawai‘i, leaving

available niche space for less desired species (Eriksson and Erlen 1992; Hurtt and Pacal 1995; Clark et al. 1999; Beckman and Rogers 2013; Peres et al. 2016). Many native Hawaiian species do not create persistent soil seed banks (Drake 1998); thus, for native plants to recruit, seed abundances need to satiate and exceed possible enemies, attract mutualists, and subsequently disperse into the areas. Comparatively, invasive alien species are either available year-round or are produce a seed bank. For example, *Clidemia hirta*, the most abundant invasive seed, produces small seeds with soft seed coats and likely does not produce a seed bank; but, fruits are available year-round (Hruska *unpublished data*). Other invasive species, such as *Rubus rosifolius and Psidium cattleyanum* (Myrtaceae), have more distinct seasonality but create a seed bank (Uowolo and Denslow 2008; Hruska *unpublished data*).

Implications for restoration

Given the variability in the composition of these novel ecosystems through space and time and a limited understanding of existing and lost mutualisms, further research is required to utilize novel ecosystems for conservation and land management purposes (Lindenmayer et al. 2008; Trueman et al. 2014). Findings here suggest that land managers and conservation practitioners in Hawai‘i should be mindful of alien birds as potential dispersers of both native and alien seeds. Foster and Robinson (2007) found that alien birds are potentially important dispersers of native seeds into degraded habitats on Maui. Since alien birds are the sole disperser of small-seeded native species on O‘ahu, perhaps increasing the abundance of small-seeded native species, while removing invasives, could increase their seed abundance, dispersal by alien birds, and subsequent regeneration (Yelenik 2016).

Hawaiian plants are poor competitors against invasive alien species, particularly in disturbed sites (*e.g.*, Cabin et al. 2002a; Cabin et al. 2002b; Loh and Daehler 2008; Cordell et al.

2009; Thaxton et al. 2012). Most Hawaiian plants have slower growth rates (Pattison et al. 1998; Baruch and Goldstein 1999; Denslow 2003) and are often seed and establishment limited compared to alien species (Loh and Daehler 2008; Cordell et al. 2009; Inman-Narahari 2013). My dissertation supports native Hawaiian plants as poor competitors against alien species and recruitment limitation as a possible mechanism. My findings also highlight small-seeded invasive understory species, *C. hirta* and *R. rosifolius*, as potentially under-rated challenges to restoration efforts on O‘ahu.

To improve native recruitment, creative solutions to reduce reproductive invasive alien species and increase native plant populations are needed (Cordell et al. 2016). Managers should continue to invest in invasive species removal even if alien species are rare or seemingly removed from the forest vegetation because alien birds disperse invasive alien seeds into native environments (Chapter 2). Additionally, native seed sowing in novel ecosystems may boost native regeneration. In Chapter 4, I used a simple field experiment to investigate suitable microsites of four common native species. Although canopy cover may not be a suitable criterion for all species, I demonstrate that it can be useful method for predicting germination and seedling success for two native species that are not being dispersed by alien birds on O‘ahu. Land managers and conservation practitioners could sow seeds of depulped *Alyxia stellata* (Apocynaceae) and *Coprosma foliosa* (Rubiaceae) under forest canopies to potentially increase recruitment of these species.

Conclusion

O‘ahu forests have been heavily altered by human colonization with many forests characterized by predominately alien species and a complete loss of native seed dispersers. In forests characterized by both native and alien species, invasive alien species are more frequently

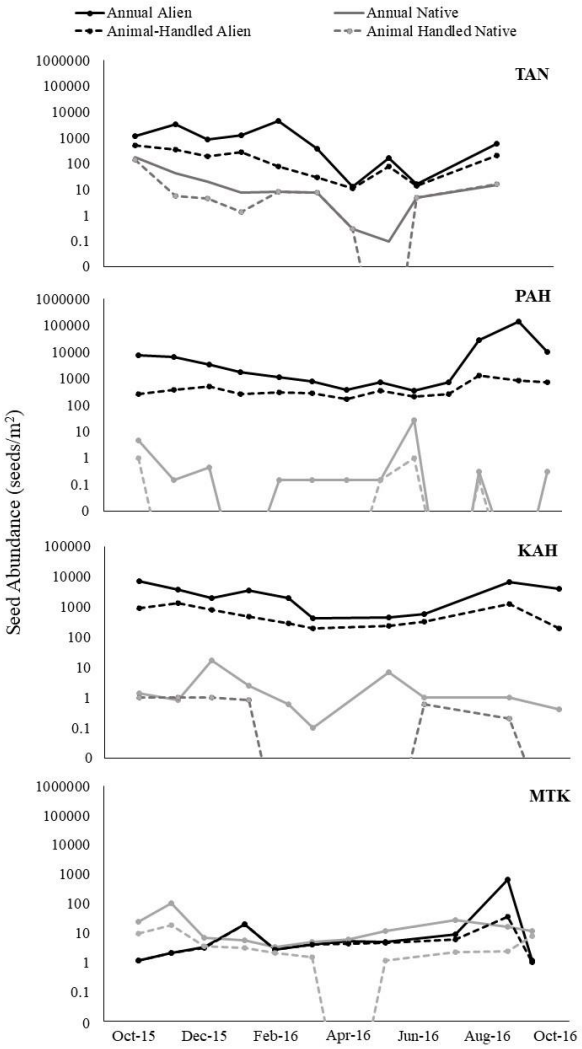
dispersed by alien birds compared to native species. These aliens represent some of the world's most invasive species, such as *Clidemia hirta, Psidium cattleyanum, Schinus terebinthefolius* (Daehler et al. 2004; Lowe et al. 2000). Common fleshy-fruited species in all forest types will probably benefit from restoration efforts, such as seed sowing, to increase native recruitment and maintain diverse forests.

Appendices

Appendix 1. The fleshy-fruited species that made up > 1.5% of cover or > 1% of the total alien or native seed rain at one or more sites, the stratum that reproductive individuals are most abundant in, seeds/fruit, and approximate seed length.

Species	Family	Stratum	Seeds/Fruit	Seed Length (mm)
Alien				
Bischofia javanica	Phyllanthaceae	> 4 m	5	2
Cestrum nocturnum	Solanaceae	2-4 m	7	3.5
Cinnamomum burmannii	Lauraceae	> 4 m	1	7.0
Clidemia hirta	Melastomataceae	0-2 m	400	0.5
Coffea arabica	Rosaceae	> 4 m	2	9.0
Ficus microcarpa	Moraceae	> 4 m	270	2.1
Hedychium species	Zingiberaceae	0-2 m	1	4.5
Passiflora suberosa	Passifloraceae	0-2 m	5	3.8
Psidium cattleyanum	Myrtaceae	> 4 m	15	5.1
Psidium guajava	Myrtaceae	> 4 m	420	4.1
Rubus argutus	Rosaceae	0-2 m	45	3
Rubus rosifolius	Rosaceae	0 - 2 m	245	1.8
Schinus terebinthifolius	Anacardiaceae	> 4 m	1	3.6
Trema orientalis	Cannabaceae	> 4 m	45	3
Native				
Alyxia stellata	Apocynaceae	0-2 m	1	14
Antidesma platyphyllum	Euphorbiaceae	2-4 m	1	8.9
Broussaisia arguta	Hydrangeaceae	0-2 m	105	0.8
Cheirodendron platyphyllum	Araliaceae	> 4m	3	5.8
Clermontia kakeana	Campanulaceae	2-4 m	1000	0.5
Coprosma foliosa	Rubiaceae	0-2 m	2	6.7
Coprosma ochracea	Rubiaceae	0-2 m	2	6.5
Cyanea angustifolia	Campanulaceae	2-4 m	200	0.5
Dianella sandwicensis	Asphodelaceae	0-2 m	9	3
Diospyros hillebrandii	Ebenaceae	2-4 m	1	13
Diospyros sandwicensis	Ebenaceae	2-4 m	1	13
Ilex anomala	Aquifoliaceae	0-2 m	11	2.3
Kadua affinis	Rubiaceae	0-2 m	10	1.1
Leptecophylla tameiameiae	Ericaceae	0-2 m	1	2.4
Pipturus albidius	Urticaceae	2-4 m	89	1.2
Psychotria mariniana	Rubiaceae	2-4 m	2	7.5
Psydrax odorata	Rubiaceae	2-4 m	2	5
Smilax melastomifolia	Smilacaceae	0-2 m	2	<10 mm
Touchardia latifolia	Urticaceae	0-2 m	1	1.9

Vaccinium calycinum	Ericaceae	0-2 m	192	1.1
Wikstroemia oahuensis	Thymelaeaceae	0-2 m	1	7.5



Appendix 2. Seed abundance and animal-handled seeds for fleshy-fruited alien and native species throughout the year by site. Sites were sampled September 2015-October 2016. Black lines represent alien fleshy-fruited species and gray lines represent native fleshy-fruited species. Solid lines represent annual seed rain and dashed lines represent animal-handled seed rain. Seed abundance is presented on a logarithmic scale to compare native (100s of seed) to alien seeds (1000s of seeds).

Appendix 3. The percentage of traps that had fruits and seeds categorized as not animal-handled and animal-handled by species. Alien species listed represent species with greater than 40% of traps with animal-handled seeds at one or more sites. Native species listed had animal-handled seeds in >3% of traps at one or more sites.

	TAN		PAH		KAH		MTK	
	Not Animal-handled	**Animal-handled**	**Not Animal-Handled**	**Animal-handled**	**Not Animal-handled**	**Animal-handled**	**Not Animal-handled**	**Animal-handled**
Clidemia hirta	6.8	94.5	49.3	100	24.1	94.4	3.3	40.7
Rubus rosifolius	0	69.3	19.3	85.3	6.5	98.1	0	2
Psidium cattleyanum	1.4	2.7	56	66	28.7	36.1	0.7	0
Schinus terebinthifolius	1.4	0	68.7	46	28.7	36.1	0	0
Brousassia arguta	--	--	--	--	--	--	1.3	20
Clermontia kakeana	0	5.4	--	--	--	--	--	--
Cyanea angustifolia	6.1	5.4	--	--	--	--	--	--
Dianella sandwicensis	--	--	--	--	--	--	1.3	5.3
Kadua affinis	--	--	0.7	0	1.8	3.7	0.7	0.7
Leptecophylla tameiameiae	--	--	0.7	1.3	--	--	42	1.3
Pipturus albidus	2.7	31.5	0.7	2	--	--	0	0.7
Vaccinium calycinum	--	--	--	--	--	--	0.7	14

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